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Programming Of Muscle Activity In Arm Movements In Relation To Force Requirements

Naznin Virji-Babul

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PROGRAMMING OF MUSCLE ACTIVITY IN ARM MOVEMENTS IN RELATION TO FORCE REQUIREMENTS

by

Naznin Virji-Babul

Neuroscience Program

Submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario
July 1995

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I look forward to hearing from you at your earliest convenience.

Yours sincerely,

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ABSTRACT

Analysis of the relationship between movement kinematics and muscle activity is a widely used approach for understanding how the nervous system formulates motor commands to produce movements. In planar single joint movements, phasic muscle activity is highly correlated with specific kinematic variables. Such correlations have not proven to be as direct in complex movements. The rules used by the nervous system in movement coordination are thus poorly understood. The purpose of this study was first, to examine kinematics, dynamics and electromyographic (EMG) activity during single and two-joint arm movements to discern the common planning strategies between these movements; and second, to gain insight into the variables used in planning complex movements.

In single joint movements made in the vertical plane, all movements were characterized by time symmetric velocity profiles. Gravitational loading directly influenced muscle activity. This suggests that basic patterns of muscle activation are modulated in relation to external forces. In two-joint planar movements involving the wrist and elbow joints, the selection of muscle activation patterns at the wrist was dependent on the relative magnitude and direction of elbow reaction torques, in relation to wrist motion. Elbow joint movement is therefore an important consideration in planning wrist movement. The details of the actual wrist trajectory may not be specifically planned, but emerges from the integration of basic patterns of activity with the dynamic interaction between joints.

The influence of visual feedback information on movement coordination was also examined. Visual feedback of the endpoint targets as well as the subject's endpoint limb position, were presented in a range of concrete to abstract representations. Changes were observed in the timing relationship between the two joints, and in the EMG patterns, in relation to visual feedback conditions.

Thus, in selecting the level and pattern of muscle activity of the distal joint during a two-joint movement, the nervous system requires information about the amplitude of the desired distal movement, and the magnitude and direction of acceleration of the proximal joint. Inter-joint coordination will further be influenced by the nature of visual feedback information.

A Word of Thanks

To these I owe a debt past telling:
My several muses, harsh and kind;
My folks, who stood my sulks and yelling,
And (in the long run) did not mind;

Researchers, past and present,
Whose findings and thoughts inspired this search;
Indeed, all those whole brains I've pressed,
Unmerciful, because obsessed;

And all those whole elbows I've twisted,
If not once, then at least a thousand times.

Adapted by A. Babul from
a poem by V. Seth

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Words cannot express the tremendous love and gratitude that I wish to extend to my parents. Their boundless love, prayers and endless encouragement empowered me to pursue my dreams. They have made infinite sacrifices to ensure that I always had access to the best opportunities.

To my husband Arif, I wish to express my love and appreciation for his unfailing belief in my abilities and for challenging me to constantly reach higher. It is with his constant support, love, encouragement (and late night physics tutorials), that I have been able to achieve my goal. For putting up with my obsessive nature and sacrificing a "normal" life, I am truly grateful.

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INTRODUCTION

One of the primary unresolved issues in motor control is the process by which the CNS translates motor planning into motor behaviour. The generation of visually goal directed actions, such as reaching towards a target, requires a transformation from a visual representation of the target location in space, into the appropriate motor commands. The rules used by CNS in transforming information from an external reference frame into an internal or motor reference frame remain poorly understood (Ghez et al, 1991). From a control perspective, the many degrees of freedom available in the upper limb poses a problem in that similar movements can be achieved in a variety of ways. As such, any one of the available paths that is chosen will involve specific commands, altering the activity of numerous muscles, to produce coordinated rotations about the shoulder, elbow and wrist joints (Hasan et al, 1985). In the face of such redundant degrees of freedom, how does the CNS select one particular path? Bernstein (1967) suggested that coordinated action may result from mastering or reducing the available degrees of freedom within the system. He further proposed that selection of particular rules or strategies would serve to simplify or optimize the task of generating appropriate signals. As a result, the search for regularities underlying the control strategies used by the CNS in coordinating limb movement continues to direct research in motor control.

The intricacies involved in human upper limb movement led many researchers in the past to restrict their analyses to single joint movements in the horizontal plane. The necessity to constrain movement in this manner to study elementary components cannot be overemphasized. These studies provided valuable information, and a sizeable body of literature now exists that describes the kinematics of single joint movements and the underlying patterns of muscle activation. Such movements, however, comprise only a small part of our normal movement repertoire. Many "natural" movements are made in the vertical plane and involve rotation about two or more joints. How then does the CNS organize such movements, and how does this organization compare or relate to the known properties of movements made in the horizontal plane? The present research was thus directed towards this fundamental question.

The study of single joint movements made in the vertical plane, is an ideal paradigm to begin an examination of the influence of more "complex" forces on movement organization. In this plane joints are subjected to torques due to the gravitational force and the magnitude of this torque does not remain constant, but change with joint angle. Furthermore, the gravitational load poses different demands for the motor system depending on the direction in which movements are made, i.e. elbow flexions are commonly made against gravity, while elbow extensions are made with gravity. Thus, in contrast to movements made in the horizontal plane, flexions and extensions made in the vertical plane are not comparable movements, each requiring specific changes in muscle torque to generate movement. This suggests that some degree of modification in the motor commands must be required to produce the respective movements.

To date, there have been very few studies that have examined both the kinematics and muscle activation patterns in this plane. Cheron and Godaux (1986) reported that elbow flexion movements made in the vertical plane were characterized by a triphasic pattern of muscle activation similar to that observed in movements made in the horizontal plane. However, Stein et al (1988) demonstrated that the pattern of muscle activity was in fact highly influenced by movements made under particular loading conditions. Each loading condition was associated with a specific pattern of muscle activity resulting in the production of quite similar movements. Given the inconsistent data on the effects of loading, single joint elbow movements made in the vertical plane were studied with the specific purpose of examining the relationship between movement kinematics and the corresponding motor commands in movements made with and against gravity.

The study of single joint movements has provided a basic framework for understanding the relationship between specific kinematic variables and the underlying motor commands. The extent to which these findings may or may not be applicable to the programming of more complex movements is a subject of considerable interest in motor control. In considering multi-joint movements there are at least two interrelated issues that must be closely examined. The first, is that rotation about two or more joints introduces specific complexities not present in the single joint case. For example, significant joint interactional effects exist between limb segments such that rotation of one joint affects movements of all other joints in that linkage (Hollerbach and Flash, 1982). These interactional forces result from reaction, centripetal and Coriolis torques and must be accounted for in order to produce coordinated movement (Bizzi and Abend, 1983). In light of this, what rules does the CNS use to produce multi-joint movements? Are the properties of single joint movements simply summated or are there completely new control processes that must be addressed when producing multi-joint movements (Bizzi and Abend, 1983; Hogan, 1985; Kaminski and Gentile, 1989)?

Recent studies have suggested that there may be some commonalities in the relationship between movement kinematics and the underlying muscle activity between single and multi-joint movements (Hong et al, 1994; Karst and Hasan, 1991; Wadman et al, 1980). However, the specific variables used in planning multi-joint movements have yet to be clearly identified. In particular, the rules used by the nervous system in selecting the appropriate pattern of muscle activation to achieve coordination between joints remain equivocal.

The second issue that must be considered is the role of visual information in movement organization. It has long been recognized that in bringing the arm to a target, motor activity is influenced by visual feedback, particularly in controlling the accuracy of movement (Jeannerod, 1988). Recently however, it has been suggested that visual information can have a much more significant role in controlling specific parameters of the movement (Cordo and Flanders, 1989), as well as in coordinating movement of limb segments during multi-joint movements (Sainburg and Ghez, 1994). How then do the properties of the external visual environment influence the planning and coordination of multi-joint movements?

In order to address the above issues, two-joint planar arm movements involving the elbow and wrist joints were studied under specific task and environmental constraints. The objective of these studies was to examine the details of the relationship between movement kinematics, dynamics and muscle activation patterns under various conditions in order to acquire a general understanding of movement planning and organization.

HISTORICAL REVIEW

In order to understand the control of voluntary movement, the study of motor control has traditionally been approached from two different perspectives. One approach has been to study movement related neuronal activity in various regions of the brain (eg. cerebral cortex, cerebellum); the other, has focused on analysis of motor behaviour, i.e. movement kinematics and dynamics, muscle activation patterns, as well as the relationships that may exist between these variables. This review will briefly summarize the important concepts that have emerged from the latter. It should be emphasized that the purpose of this approach is to reveal the existence of consistent relationships in measured variables. Such relationships are then used to *infer* the rules used by the CNS, as well as the variables that are directly controlled, in planning and producing movement.

The concepts to be discussed in this section will be presented in a historical context and will trace the development of motor control research beginning with the study of single joint movements, followed by a discussion on multi-joint movements. The primary objective of this review is to highlight the similarities and differences that are thought to underlie the control and generation of single and multi-joint movements.

1.1 Classification of Movements

For many years, one of the most widely used classification of movements was based on speed, with movements classified as either slow or fast (Stetson and McDill, 1923). Fast movements were thought to be characterized by a stereotyped pattern of phasic muscle activation (Wacholder and Altenburger, 1926). A lack of phasic activity characterized slow movements. Interestingly, this distinction was extended to distinguish between the mechanisms underlying the generation of the two classes of movement. Fast movements were considered to be preprogrammed since there was little time for feedback to influence the movement. Modification of fast movements were thought to be achieved by changes in the initial "set" of the motor system prior to the start of movement. In contrast, slow movements were presumed to represent a closed-loop system, modified by peripheral input (Stetson and McDill, 1923; Stetson and Bouman, 1935).

The terminology of fast and slow movements permeated much of the early motor control literature. This distinction however, was not useful in characterizing movements over a wide range of speeds as well as movements which included both a fast and slow component. As movements over a range of speeds and task conditions were studied, specific kinematic relationships were discovered which became associated with a distinct class of movement. These kinematic features were first observed in single joint movements made in the horizontal plane and will be discussed below.

1.2 Single Joint Movements

A. Kinematic characteristics

Many movements about a single joint have been characterized by a smooth, bell shaped velocity profile in which the duration of the acceleration and deceleration phases are approximately equal. This relationship remains invariant with changes in both movement amplitude and duration (Cooke et al, 1989; Morasso, 1981; Ostry et al, 1987). In normal subjects a linear relationship has been observed between peak velocity and movement amplitude (Bouisset and Lestienne, 1974; Cooke, 1980). In addition, movement duration has been found to increase with amplitude (Benecke et al, 1985; Brown and Cooke, 1984).

It has been argued that this basic velocity profile may be limited to a specific class of "artificial" movements (Jeannerod, 1988). Marteniuk (1987) has shown for example, that grasping movements involve a longer deceleration phase compared to the acceleration phase. Although the velocity profile may be temporally asymmetric in movements requiring a high degree of accuracy (Soechting 1984; Gentilucci et al, 1991), time symmetric velocity profiles have been observed in many well-learned movements, including single joint movements in the vertical plane (Atkeson and Hollerbach, 1985), multi-joint movements (Morasso 1981; Soechting 1984; Kaminski and Gentile, 1986), speech movements (Ostry, 1986) and movements of the vocal folds (Munhall et al, 1985).

The observation that the form of the velocity profile remained invariant under transformations of movement amplitude and speed, led to the suggestion that these movements belonged to an equivalence class of movements that were produced through similar organizational rules. In particular, the consistent peak velocity and movement duration relations under transformations of movement amplitude and speed, suggested that these relations may be fundamental organizing principles underlying movement. The question that arises is what parameter(s) is controlled or optimized to produce this class of movement? A number of theories have been put forth suggesting that the temporally symmetric form of the velocity profile may arise through minimization of energy (Nelson, 1983), optimization of joint stiffness (Hasan, 1986) or by minimizing the rate of change of acceleration, i.e. jerk, (Hogan, 1984).

However, Stein et al (1988) have shown that minimization of jerk may not be a general principle used to organize movements. Movements made under elastic, viscous and inertial loads were compared with calculated trajectories based on minimizing acceleration, jerk and energy consumption. Although the data from movements made under the inertial loading conditions correlated well with minimum jerk predictions, systematic deviations were observed for movements made against elastic and viscous loads. In addition, the data were not consistent with trajectories that would correlate with minimization of energy consumption.

The authors argue that the good correlation of the inertial load trajectory with the predicted minimum jerk trajectory, may be explained simply by the fact that inertial loads act as mechanical low-pass filters. Thus, mechanical damping may result in a smooth movement that approaches the predicted trajectory. They further propose that the CNS may generate simple waveforms of EMG activity that are adjusted to meet the requirements of the task based on trial and error, rather than through precise computations based on minimizing kinematic variables or energy consumption. The nature of EMG activity and the relationship between individual bursts of phasic activity and kinematic parameters will be discussed in subsequent sections.

B. Relationship between EMG and force

A commonly used measure that provides an indication of the neural commands to a muscle is an electromyogram (EMG) (Hasan et al, 1985). The electromyograph essentially detects and records electrical activity that is associated with the activation of muscle fibers by their motorneurons. It should be noted that surface electrodes detect the activity of many motor units (i.e. the motor neuron and all the muscle fibers innervated by that axon) at the same time (Loeb and Gans, 1986). The relationship between the EMG signal and the force output of the muscle is quite complex and is influenced by a number of factors related to the mechanical properties of muscle fibers which are briefly discussed below.

(i) Properties of Muscle

The sarcomere, the smallest contractile unit, is composed of two proteins: thin (actin) and thick (myosin) filaments. During muscle contraction the heads of the myosin molecules attach to receptor sites on the actin molecules, producing cross bridges between the thick and thin filaments. Contraction occurs when the myosin molecules slide over the actin molecules. Gordon et al (1966) discovered that the magnitude of active tension that developed during contraction was dependent on sarcomere length, or more specifically, the extent of filament overlap. Thus, if the sarcomere is stretched beyond the length at which the filaments overlap, cross bridges cannot form and tension cannot develop. Maximal contractile tension develops when there is maximal single overlap between the actin and myosin filaments.

As a first approximation, a simplified model based on the properties of a spring can, in general terms, explain the behaviour of muscle (Nichols and Houk, 1976). An increase in the length of a spring will result in the production of a restoring force that is proportional to the change in length. Tension increases linearly once the length exceeds the set point or resting length. The slope of this relationship defines the elastic or static stiffness of the spring. The length-tension curve of a muscle is different from a spring in that this relationship is not linear but has an inverted U shape with maximum force produced at the muscle's resting length. The muscle tension at a particular length is dependant on both stiffness and resting length.

Muscle tension is also dependent on the rate of muscle shortening or lengthening. Muscle tension decreases during concentric (shortening) contractions and increases during eccentric (lengthening) contractions. As the shortening velocity increases, muscle tension decreases and increases as lengthening velocity increases (Winter, 1991).

(ii) EMG activity in isometric and isotonic movements

The relationship between EMG and muscle tension was first studied in isometric contractions. Lippold (1952) and Miller-Brown and Stein (1975) have shown that there is a linear relationship between integrated EMG and muscle tension. Bigland and Lippold (1954) further showed that during isotonic contractions there is a linear relationship between integrated muscle activity and tension during constant velocity shortening and lengthening contractions. Although there is evidence that shows a linear relationship between integrated EMG activity and mechanical work during isotonic movements (Bouisset and Goubel, 1973), the precise relationship between EMG and force during dynamic conditions is not known (Hannaford and Stark, 1985). At present, the EMG signal is thought to roughly predict muscle tension under conditions where muscle length is not rapidly changing (see Loeb and Gans, 1986; Winter, 1991).

C. Relationship between individual EMG bursts and specific kinematic parameters

The muscle activation pattern associated with fast movements was first described by Wacholder and Altenburger (1926). This pattern consists of a burst of activity in the agonist muscle followed sequentially by a burst of activity in the antagonist, and a second more prolonged burst of agonist activity. This basic triphasic pattern of alternating agonist and antagonist activity has since been reported in a wide range of single joint movements of varying amplitudes and has been shown not to be limited to simply fast movements (Angel et al, 1965; Brown and Cooke, 1981; Ghez, 1979;

Hallett et al, 1975; Hallett and Marsden, 1979; Lestienne, 1979).

Since the original description, the role of each component as well as the control and generation of this EMG pattern, has been the subject of much study, particularly in relation to single joint movements. In particular much of the early work in this area was directed towards uncovering relations between the individual phasic bursts of EMG activity and specific kinematic variables such as movement amplitude, velocity and acceleration. The aim of this section is to review the function of each individual burst and summarize the EMG-movement relationships that were proposed as well as the generation of the pattern.

(i). Initial Agonist Burst

The initial agonist burst (AG1) starts prior to movement onset and provides the force necessary for accelerating the limb (Woodworth, 1899; Stetson and McDill, 1923; Angel, 1974; Hallett and Marsden, 1979). For many years it was thought that AG1 was largely preprogrammed since its duration remained constant in isotonic as well as isometric movements of different amplitudes (Brown and Cooke, 1981; Freund and Budingden, 1978; Ghez, 1979; Hallett et al, 1975;). The implication was that movement velocity and amplitude were controlled simply by modulating burst amplitude. However, later studies that examined a wider range of movement amplitudes and analyzed changes in individual as opposed to averaged records of phasic bursts revealed that AG1 duration was in fact modulated with movement amplitude (Berardelli et al, 1984; Brown and Cooke, 1984; Wadman et al, 1979). This finding led to the suggestion that the nervous system could regulate both the amplitude and duration of the initial agonist burst to produce movements of different velocities and amplitudes.

(ii). Antagonist burst

Although the function of the phasic antagonist (ANT) burst has been assumed to be related to the force necessary to decelerate the movement (Lestienne, 1979; Marsden et al, 1983), the generation and control of this burst is not fully understood. Based on their observations that phasic antagonist activity was not present during isometric movements, Ghez and Martin (1982) proposed that phasic activity in the antagonist represented a stretch reflex response that was dependent on movement of the limb. They further showed the timing of the antagonist activity remained the same during both active and passively imposed movements. A number of other studies showed however, that the process of braking is incompatible with a reflex response. Activity in the antagonist was observed prior to the end of the initial agonist burst (Hallett et al, 1975) and before there was significant displacement of the limb (Angel, 1977). Both the timing and magnitude of antagonist activity were found to be dependent on movement amplitude, speed (Marsden et al, 1983), instruction (Brown and Cooke, 1981) and strategy (Waters and Strick, 1981).

It was further observed that large amplitude movements were associated with decreased antagonist activity while small amplitude movements were associated with greater activity (Flament et al, 1984; Marsden et al, 1983; Meinck et al, 1984). Little or no activity in the antagonist was observed in movements that were stopped mechanically (Marsden et al, 1983). Marsden et al (1983) proposed that since viscoelastic forces which restrict speed of the movement, are larger at the extremes of joint rotation, less antagonist activity would be required to brake the movement in small movements made in the mid-range of rotation. However, Flament et al (1984) found similar results although all amplitude movements were subjected to the same viscoelastic forces. They argue that the larger antagonist burst in small amplitude movements (that were made at the same peak velocity as larger amplitude movements), is produced to maintain a symmetrical relationship between the acceleration and deceleration phases of the movement. Although the function of this burst remained controversial, it was apparent that the timing and amplitude of ANT was influenced by movement velocity (Marsden et al, 1983), limb inertia (Flament et al, 1984) and instruction (Meinck et al, 1984). This led to the suggestion that ANT was in fact centrally mediated and influenced by peripheral events.

(iii). Second agonist burst

In comparison with AG1 and ANT, the second agonist burst (AG2) has received very little study. Based on the work of Jansen and Rack, (1966) and Joyce and Rack (1969) which showed that stretch reflex activity increases muscle stiffness in response to a sudden deflecting force and resists the disturbing force, Ghez and Martin (1982) proposed that AG2 was a stretch reflex response that served as a damping mechanism to reduce oscillations at the end of movement. Hannaford and Stark (1985) studied the role of each pulse by computer simulations in which they selectively removed pulses from the control signal. In removing the second agonist pulse they found that although the correct final movement was achieved initially, this target position was not maintained. They proposed that AG2 is a clamping pulse to maintain the limb in the final position.

(iv) Control of individual bursts

Studies on deafferented patients has shed some light on the controversy between central and peripheral control of individual bursts. A number of investigators found that there is no difference in AG1 duration between normal subjects and deafferented patients performing the same task (Rothwell et al, 1982; Hallet et al, 1975;). Cooke et al (1985) further showed that the duration of the agonist burst increased with movement amplitude in one deafferented patient, as in normal subjects. Forget and Lamarre (1987) observed that phasic activity in both the antagonist, and the second agonist was present during single joint elbow movements performed by deafferented patients. They did note however, that there were changes in the timing and magnitude of the antagonist burst. Furthermore, Brown and Cooke (1986) found that in normal subjects, randomly applied perturbations applied prior to the onset of movement, resulted in modifications of the initial agonist burst. Taken together, these studies argue against the hypothesis that the individual components of muscle activity are entirely under peripheral control. However, sensory feedback certainly does play an important role in fine tuning muscle activity in relation to task conditions.

D. Current concepts of movement generation

In reviewing the studies discussed above, it appears that the correlations of individual bursts of phasic muscle activity with single kinematic variables are at times quite disparate and somewhat conflicting. Essentially, there has not been a unifying theme with which to understand the fundamental relations underlying these correlations. In recent years, there has been a concerted effort to move from isolated descriptions of individual components of muscle activity, to consolidating various observations under the broader context of movement generation from kinematic and kinetic perspectives as well as on the basis of behavioural constraints.

Ghez and Gordon (1987) have approached this problem by studying the relationship between EMG bursts and the dynamics of the force trajectory under isometric conditions. They found strong correlations between specific parameters of the force trajectory and EMG activity. For long force rise times, the rising phase of the trajectory was controlled simply by regulating agonist activity. An alternating pattern of activity in the agonist and antagonist was affiliated with short rise times. Thus, they proposed that activity in the agonist initiates force development while activity in the antagonist serves to decelerate, or more specifically, to control the rising phase of the force trajectory.

In terms of isotonic movements, Hoffman and Strick (1986; 1990) proposed that the initial trajectory of single joint movement can be specified simply by controlling two kinematic variables: peak magnitude and duration of a derivative of displacement (i.e. acceleration or jerk). By independently adjusting the parameters of these variables, movements of different amplitudes and speeds can be produced. Specifically, changing derivative magnitude alters movement amplitude and both variables are modulated to adjust movement speed. They further suggest that these two kinematic variables are generated by independently controlling separate bursts of muscle activity. Modulating the magnitude of the agonist burst controls the magnitude of a derivative of displacement, while adjusting the magnitude of the antagonist burst controls the duration of a derivative of displacement.

The flaw in this proposal is that the evidence has been obtained from studies of rather constrained movements. Step tracking movements generally are characterized by temporally symmetrical profiles and it is questionable therefore whether these parameters reflect global principles and apply to movements of different temporal structures.

In this respect, Cooke and Brown (1986) recently developed a phase-plane tracking paradigm in which the temporal structure of a movement could be precisely controlled and thus movements of different temporal structures could be examined. Using this technique they demonstrated that the components of phasic muscle activity are strongly correlated with the duration of acceleration and deceleration (Cooke and Brown, 1990). By temporally separating acceleration from deceleration by introducing different periods of constant velocity, they found that paired activation of opposing muscles were associated with each component of acceleration and deceleration, respectively. Furthermore, as the period of constant velocity decreased, the pairs merged to form the classic triphasic EMG pattern to produce movements having a smooth transition from acceleration to deceleration. This finding demonstrates that movements that do not belong to the same equivalence class are produced by modulation of the classic triphasic pattern. In addition, Cooke and Brown (1994) recently showed that acceleration duration varies directly with AG1 duration in a wide range of different movements. Since in an inertial model acceleration is directly related to force (which in turn is reflected in the EMG), this suggests that acceleration duration may be used as an approximation in selecting muscle activation patterns in planar, single joint movements.

Gottlieb et al (1989) have proposed yet an alternative hypothesis in which the control of movement is based on a set of rules that are determined by task demands. Limb movements are essentially thought to results from shifts of the equilibrium point that result from changes in the threshold of length-sensitive reflexes of each participating muscle. The actual changes in muscle length, tone and EMG are thought to depend on central commands as well as the load or task conditions. Movements are classified according to a speed insensitive (SI) strategy or speed sensitive (SS) strategy. Thus, the parameters of motorneuron excitation are thought to be modulated on the basis of individual strategies and consequently the EMGs and kinematics change as a result of this modulation. The control signal is modelled as a rectangular excitation pulse in which the pulse width or pulse height is modulated depending on the movement strategy. Phasic EMG bursts are regarded as low-pass filtered versions of the excitatory pulses that are applied to the motorneuron pools by the nervous system (Gottlieb et al, 1990).

In pulse width control, the width of the excitatory pulse is modulated. Thus, in the SI strategy, pulse duration or width is thought to be modulated during movements made over different distances or loads with no explicit constraints on the speed or time of movement. This strategy gives rise to EMGs that have the same rate of rise, regardless of changes in distance or load. The duration of the phasic burst is modified by changes in the task. When explicit control is exerted over speed (SS strategy), pulse height is modulated. In pulse height control, the height of the excitatory pulse is modulated while the duration remains constant. The amplitude of the pulse determines the rate at which the EMG activity will rise. Thus, in this case, the area and the initial slope of the EMG will be modulated. Essentially then, the movement trajectory and the agonist EMG arise as a consequence of the preprogrammed commands. Although the timing of the antagonist EMG burst is also thought to be preprogrammed and based on the kinetic demands of the task, a single rule that explains this latency has yet to be defined (Gottlieb et al, 1992).

E. Summary

The studies described above have provided a basic framework for understanding the variables used by the CNS to control the features of single joint movements. The relationship between phasic activity and the production of movement remains controversial. At present, there appear to be essentially two basic views. One view emphasizes the importance of behavioural strategies, suggesting that the nervous system controls parameters of the motorneuron excitation pulse on the basis of task constraints, resulting in predictable changes in EMG and kinematic variables (Gottlieb et al, 1989). The other view takes the perspective that the nervous system modulates the EMGs in order to produce very specific movement or force trajectories (Brown and Cooke, 1990; Ghez and Gordon 1987; Hoffman and Strick, 1986; 1990). The issue of significant interest is to determine whether the relationships described by the proponents of the respective theories are applicable simply to single joint movements, or whether in fact, they reflect more general principles of movement generation that are relevant in understanding more complex movements. Thus the basic question that must be addressed is, can the problem of understanding limb movement control be solved by understanding the control of single-joint movement?

1.3 Multi-joint movements

The study of multi-joint movements introduces a number of interesting problems that are not present in the single joint case. Unlike movements about a single joint, the torques acting at each joint in a multi-joint link do not arise simply from the muscles acting about that particular joint. Rather, rotation of one joint affects the movement of all other joints in that linkage, and gives rise to reaction, centripetal and Coriolis torques (Bizzi and Abend, 1983) the magnitudes of which can be quite significant over a range of movement speeds and trajectories (Hollerbach and Flash, 1982). Given the dynamic complexities of multi-joint movements, the question that arises is how such interactional effects are accounted for, and more specifically, what the nature of the relationship is between movement kinematics, dynamics and muscle levels of control. In this section these different levels of control will be discussed.

A. Movement Kinematics

One of the primary unresolved issues in multi-joint movement control is the identification of the space or reference frames in which movements are represented. The significance of this issue becomes apparent when comparisons are made with the single joint situation. In a single joint movement about the elbow, the hand is mechanically constrained to moving in a curved path. In contrast, during multi-joint movements, the hand can move along various paths to reach a target. As such, the trajectory of the hand may be planned either in terms of end point or joint angle coordinates (Hollerbach, 1990). The minimum jerk theory proposed by Flash and Hogan (1985), proposed that upper limb movements are planned in terms of endpoint coordinates, with the handpath selected on the basis of minimizing jerk. Hogan (1987) further showed that minimizing jerk always results in a straight line handpath. In planning movements in terms of the endpoint, the CNS must then compute the joint angles over time, using complex, inverse kinematic transformations. In contrast, the joint interpolation theory proposed that limb movements are planned in terms of joint variables (Hollerbach, 1990). In this view the limb is represented as a two-link planar manipulator consisting of the shoulder and elbow joints, and two links consisting of the upper arm and forearm. The manipulandum configuration is determined by the shoulder and elbow joint angles plotted in joint space. The CNS is thought to compute the joint angles required to achieve the final hand position, plotting a course along a straight line in joint space (which results in curved handpaths). The hand positions are calculated from joint angles using less complex, direct kinematic transformations (Hollerbach, 1990).

An early study by Morasso (1981) supported the theory that movements were planned in terms of endpoint coordinates. When asked to move their hand from one target to another, subjects generally produced straight hand paths. Compared with other joint trajectories, only the hand trajectory was characterized by a smooth, bell-shaped velocity profile. Very little variability was exhibited in this motion with changes in movement duration or location in the workspace. Based on these results Morasso (1981) argued that the CNS must plan movements in terms of hand kinematics and subsequently transform this plan into joint coordinates. Straight line paths with consistent movement trajectories of the hand were also found by Soechting and Lacquaniti (1981) in a pointing task. In addition, they found that peak velocity of both the shoulder and elbow was reached at the same time and elbow and shoulder velocity were related to each other in a linear fashion in the deceleratory phase. The authors proposed that pointing movements may in fact be planned in terms of hand trajectory, but that this trajectory must be constrained to maintaining a specific relationship between the moving joints.

In order to further examine joint relationships, arm movements during a reaching task involving the shoulder, elbow and wrist joints were analyzed, with the objective of determining whether shoulder-elbow coupling remained invariant when an additional degree of freedom was added to the system (Lacquaniti and Soechting, 1982). Interestingly, while the shoulder and elbow relationship remained the same in this task, no consistent relationship was observed between the wrist and the two proximal joints. In fact, the motion at the wrist was quite variable in both timing and duration. Lacquaniti and Soechting (1982) argued that motion at the elbow is inertially coupled with that of the shoulder and serves to reduce the degrees of freedom that need to be controlled. In contrast, the wrist joint may be regulated independently as it not functionally related to the proximal joints.

The concept of a strategy based largely on controlling joint relationships has been developed in various forms by a number of investigators. Atkeson and Hollerbach (1985) examined trajectories of arm movements made in the vertical plane. In contrast to the previous studies, they observed both straight line and curved paths. Path curvature was dependent both on direction of the movement and area of workspace. In some subjects upward movements were more curved than movements in the downward direction. A common bell shaped velocity profile was observed in all movements. The authors proposed a planning strategy based on staggered joint interpolation, i.e. the time at which joints start or stop moving may be staggered or delayed with respect to each other, with a common movement profile observed at all joints. This strategy was thought to be more advantageous in that it required less complex, direct kinematic transformations (Hollerbach, 1990).

Kaminski and Gentile (1986) also reported curved hand paths during multi-joint pointing movements in the horizontal plane. Furthermore, the time of movement onset between elbow and shoulder joints was staggered, and this difference was dependent on joint displacement, i.e. the joint that moved the furthest, moved first. Using computer simulations they demonstrated that this staggered timing was crucial for producing a smooth velocity profile. When onset times were shifted so that both joints started moving at the same time, significant alterations were produced in the shape of the velocity profiles. More importantly, a high correlation was found between peak velocity and displacement for both joints. The authors suggest that coordination of multi-joint movements is simplified by maintaining a linear relationship between peak velocity and amplitude, and by use of a space-time transformation to regulate the onset of joint movement.

Kaminski and Gentile (1989) further compared multi-joint movements of the shoulder and elbow to single joint elbow and shoulder movements. The trajectory of the hand was found to remain consistent, regardless of whether motion involved single or multi-joint movement. In addition, the relationships between peak velocity and amplitude and movement duration and amplitude, at the shoulder remained consistent in all conditions. However, significant changes were observed at the elbow joint such that the kinematic relations observed in single joint elbow movements changed during multi-joint movements to resemble those of the shoulder joint. The authors suggest that during pointing movements, organization of arm movements may be structured at two levels. Planning of hand trajectory is of primary importance. A secondary strategy is also used which takes place at the joint planning level to simplify coordination between joints.

The studies outlined above are primarily based on movement analysis at a kinematic level. In this respect, many similarities have been found between the point to point kinematic relations observed in single and multi-joint movements. In terms of movement planning, straight line paths have provided evidence for planning in endpoint coordinates. Curved paths and coordination between joints and suggest planning in terms of joint coordinates; however, the mechanisms by which joint movement onsets are regulated remains very unclear. Certainly a thorough analysis of multi-joint movements must include a study of the motor commands underlying these movements.

B. Muscle activation patterns associated with multi-joint movements

One of the first descriptions of the muscle activation patterns in multi-joint movements was provided by Wadman et al (1980) in a study of two-joint movements involving the shoulder and elbow joints. Hand trajectories were characterized by curved paths and smooth bell shaped velocity profiles. Interestingly, a triphasic EMG pattern was observed, similar to that reported in single joint movements. Since this study, a number of investigators have reported that many multi-joint movements are associated with a basic pattern of muscle activation consisting of alternating EMG bursts in the agonist and antagonist at each joint (Accornero et al, 1984; Karst and Hasan, 1991; Hong et al, 1994). However, a number of task dependent modifications have been observed in the EMG-movement relations.

In an early study, Lacquaniti and Soechting (1982) found that during reaching movements, the pattern of activity in the biceps was modulated on the basis of the direction of forearm rotation and on movement speed. In addition, the pattern of EMG activity was dependent on movement direction (Soechting and Lacquaniti, 1981). Specifically, both the magnitude of the AG1 (Wadman et al, 1980) as well as the time of onset of muscle activity (Flanders, 1991) are dependent on movement direction.

Karst and Hasan (1991) also reported a number of interesting differences in the muscle activation pattern. They established that the sign of the initial agonist activity does not necessarily correlate with the direction of joint rotation, i.e. in certain elbow extension movements, activity in the biceps was activated prior to the triceps. In general, the sign of the agonist appeared to vary with the target direction relative to the initial orientation of the distal segment. In addition, the magnitude of the initial agonist burst at the elbow joint was modulated to a much greater extent than that reported in single joint movements. In some directions, no activity was present in the agonist. Rotation of the elbow was thought to be produced by interactional torques resulting from shoulder rotation.

Koshland et al (1991) have shown further that during voluntary and imposed movements of the elbow joint, muscle activity at the wrist joint acts to minimize the effect of the reaction forces at that joint resulting from elbow movement. Such activity is present regardless of whether the wrist is immobilized or free to move, suggesting that there may be specific coupling of elbow and wrist activity under certain task conditions where voluntary movement of the wrist is not required. Darling and Cole (1990) have also shown that compensatory strategies are directly influenced by the type of movement required at each joint. In studying index finger movements they found that muscle activity was not dependent exclusively on movement speed, but was in fact modulated on the basis of the type of movement required at each joint, i.e whether each joint in the link was actively moving or was maintained at a constant joint angle. Each condition was associated with changes in muscle activity that were directly related to compensatory strategies required to counteract segmental interactional torques.

Given that muscle activity is modulated on the basis of task requirements, what rules are used by the CNS in selecting appropriate muscle activation patterns? Thus far there have been few attempts at systematically addressing this question. Koshland and Hasan (1994) have advanced the importance of positional variables in multi-joint movement planning. They observed that the selection of initial muscle activity was correlated with target location and that altering the relative joint amplitudes did not affect this activity. Karst and Hasan (1991) have further proposed that the nervous system uses relatively simple rules to select muscle activity based on positional variables, and does not explicitly take into account the torques resulting from the dynamic interactions of the various limb segments. Thus errors resulting from inadequate prior compensation would be corrected by appropriate sensorimotor responses as movement progresses.

C. Summary

In recent years the study of the control of arm movements has dramatically shifted from analysis of single joint to multi-joint movements. Understanding of multi-joint planning and generation is at an early stage where identification of relevant control variables are only just emerging. In pursuing this study, there has been much discussion about the relevance and applicability of findings from single joint studies to multijoint movements (see commentaries in Gottlieb et al, 1989). However, to date, there have been few attempts to integrate and link the two bodies of literature in an effort to determine whether any commonalities exist between the strategies used by the CNS in planning single and multi-joint movements. From this review, it would appear that there are indeed common fundamental concepts which should not be disregarded, and could in fact, be used as a platform from which to begin more detailed analyses of multi-joint movements. It must be emphasized however, that multi-joint movements introduce new issues for consideration and demands an extensive study of the inter-relationship between movement kinematics, dynamics and muscle activity.

1.4 Models of movement generation and control

In order to unify experimental observations, a major focus of motor control research has been directed towards developing models to explain movement planning and organization. In studying the historical evolution in motor control, it is interesting to note that many of the early theories or models were expressed in terms of descriptive rules or mathematical statements relating one measured kinematic or kinetic variable to another (eg. Fitt's Law). This was followed by descriptive rules that explicitly considered muscle activity and attempted to relate specific components of phasic muscle activity to kinematic and/or kinetic parameters (eg. pulse-step model). More recently, as interest grew in studying more complex movements, there has been a definite shift from considering the relationship between isolated variables, to developing more global approaches that attempt to integrate the influence of afferent input (eg. vision), feedback, and task conditions, on movement planning. In particular, the emphasis is now on understanding the complex process by which the nervous system integrates information from the external environment and converts the plan of an intended movement into the appropriate commands to produce that movement. The purpose of this section is to summarize this historical development by briefly outlining key models that have influenced the understanding of movement generation.

A. Models of the Speed-Accuracy Trade-off

One of the earliest attempts to describe and establish relationships between kinematic variables during movement was by Woodworth (1899). Woodworth (1899) performed detailed experiments in which he asked subjects to reproduce the length of a line under specific experimental conditions, in order to examine the effects of speed, repetition frequency, and vision on movement accuracy. From these detailed experiments he concluded that discrete movements consisted of two phases: an initial impulse phase and a current control phase. During the initial impulse phase the arm rapidly moves towards the target in what he considered, a reflex mediated response. The second, current control phase was described in terms of "extra corrective movements" that rectified deviations from the intended movement path. The ability to make these corrective movements was dependent both on the total time permitted for the movement as well as on visual feedback. Fast movements would therefore be less accurate. Interestingly, Woodworth (1899) hypothesized that the initial impulse phase would require the "innervation of different muscles one after another and that it included the command to stop after a certain distance" i.e. that this command would control movement amplitude.

The relationship between speed and accuracy of movements was further studied by Fitts (1954) who corroborated Woodworth's basic findings. In his experiments, subjects were asked to hit targets of different widths, separated by specific distances, using a stylus. For any given target width, movement duration increased with movement amplitude. Furthermore, for a given distance between targets, movement duration increased as target width decreased. This relationship between movement speed, accuracy and amplitude was described by a logarithmic function. It should be noted that Fitts' Law does not apply to movements made in the absence of visual feedback (see Jeannerod, 1988).

Fitts ascribed the speed-accuracy trade-off to the noise in the sensorimotor channel. The time required to produce an accurate movement was presumed to be based on the amount of information that had to be transmitted in producing that movement. Assuming that the transmission channel is noisy, the more information to be transmitted (eg. the more difficult or demanding the task), the longer time would be required to extract the signal from the noise. This explanation has since been disregarded and a number of other interpretations have been postulated to explain Fitts' Law.

Crossman and Goodeve (1963) proposed that movements to a target were made of a series of sub-movements that were all modulated by visual feedback. Keele (1968, 1981) further proposed that the duration of the initial movement was not subject to feedback correction and should be independent of movement amplitude and precision. Discrete submovements have been observed by a number of investigators (Crossman and Goodeve, 1963; Brooks et al, 1973). However, corrective movements have not been observed in large amplitude movements (Langolf et al, 1978). In addition, this model cannot explain accuracy in movements made without visual feedback (Bizzi et al, 1976). Recently Cordo (1987) has shown that during single joint isometric contractions, changes in torque may in fact be mediated by three different control mechanisms. In these movements, the initial rise in torque was guided by information from the visual stimulus. Corrective adjustments of the force trajectory were produced from visual information about target location. Visual and kinaesthetic information subsequently produced the final corrective adjustments.

B. Impulse-variability model

Another interpretation of Fitts' Law has been proposed or the basis of variability in muscle generated force impulse (Schmidt et al, 1979; Meyer et al, 1982). Since faster movements require larger force impulses and are associated with greater end point variability, it was suggested that motor output variability is proportional to the size of the motor output. The assumption underlying this proposal is that motor commands are preprogrammed with little or no modulation by feedback, and are characterized by an invariant force-time function that is scaled according to the task. Equal preprogrammed phasic impulses are assumed to explicitly control the acceleration and deceleration phases of the movement resulting in the producing of a symmetric velocity profile (Meyer et al, 1982). However, since these original experiments, it has subsequently been demonstrated that different tasks can in fact, be associated with asymmetrical velocity profiles (see Jeannerod, 1988). Indeed, Brown and Cooke (1990) have also shown that the same movement task can be accomplished with virtually any trajectory. In addition, Darling and Cooke (1987) showed that variability in movement trajectory was greater during the deceleration phase in comparison with the acceleration phase and suggesting that feedback from the initial phase of the movement is important in modulating the antagonist activity to correct the initial errors.

C. Speed-control and Pulse-step models

Two other similar models were also proposed that advanced the hypothesis that movements resulted from preprogrammed motor commands. These models attempted to relate specific EMG activity with kinematic and kinetic movement variables. The basis for this hypothesis came from early studies that indicated that the duration of the initial agonist burst was invariant. Freund and Budingden (1978) developed a speed control hypothesis in which they stated that movements of different amplitudes were generated by modulating AG1 magnitude and maintaining a constant movement duration.

The pulse-step model incorporated and accounted for the control of the final limb position (Ghez and Vicario, 1978). Essentially, an initial pulse of activity of fixed duration is followed by a tonic command. This initial phasic command was thought to determine the rate of force change in isometric movements or the limb trajectory in isotonic movements. For isometric movements the tonic command was thought to be important in maintaining the final steady force; for isotonic movements, the final position of the limb. The pulse-step model was originally proposed in relation to eye movements. Robinson (1970) showed that in order to move the eye towards a target, a pulse-step change in excitation is required to overcome the viscous drag and the elastic restoring forces of the orbital contents. The low mass of the eye makes inertial effects negligible. The pulse (velocity) command causes a phasic contraction of the extraocular muscles which results in a rapid movement of the eye towards the target. The subsequent step (position) command causes a tonic contraction that serves to overcome the elastic restoring forces and holds the eye in the new position. This model however, cannot adequately explain limb movements where inertial forces are dominant. In addition, the validity of both the above models in relation to limb movement have been challenged by the finding that the duration of the initial agonist duration is not fixed and can in fact, be modified by task requirements (Berardelli et al, 1984; Wadman et al, 1979; Brown and Cooke, 1984; 1990; Cooke and Brown, 1994).

D. Models incorporating kinematic and dynamic transformations

In recent years there has been considerable interest in studying the planning and execution of multi-joint movements. One hypothesis is that a hand trajectory in extrinsic space is converted into a trajectory in joint space through kinematic and dynamic transformations (Hollerbach, 1990). Specifically, given a desired hand position, the corresponding joint angles required to achieve that position are produced by solving inverse kinematic equations. As has been discussed previously (see section on kinematics of multi-joint movements) evidence for planning in kinematic coordinates has been provided from studies showing consistent relationships in endpoint (Morasso, 1981; Abend et al, 1982) as well as joint angle variables (Hollerbach, 1990; Soechting and Lacquaniti, 1981; Kaminski and Gentile, 1986).

Given the joint angles, the appropriate torques must then be applied to the joints in order for the limb to move along a particular trajectory. The time sequence of joint torques is determined by solving inverse dynamic equations. These joint torques are subsequently transformed into muscle forces and the necessary muscle activations, and are corrected by feedback based on position and force errors (Hollerbach, 1990).

How might the system compute such joint angles and torques for a desired trajectory? Atkeson (1989) has suggested that successful transformations may be achieved by building internal inverse limb models that may be based either on formulating look-up tables, (i.e. inverse dynamics would be solved by looking up joint torques on the basis of desired joint positions, velocities and accelerations) or on structured representations, such as a computer program. In both cases, performance errors may be corrected by feedback and by learning through practice to update the model.

Tabular representations can be generalized to numerous transformations. The constraint however, is that many parameters must be specified. In contrast, only a few parameters must be specified in structured representations to describe the transformation; however, the model would be constrained to specific transformations. Atkeson (1989) has reviewed a number of structured approaches used to build theoretical dynamic models by approximating inertial parameters such as mass, location of centre of mass and moments of inertia. Such models have been "implemented" on robots with good matches obtained between predicted and actual torques.

The question that arises is that if the CNS does perform inverse dynamic computations, how accurately are the estimates of the inertial parameters represented? It has been suggested that slight alterations in inertial parameters can result in rather large errors in movement; hence, it would seem implausible that the CNS could perform such precise computations so quickly (Hasan, 1991; Bizzi et al, 1992). Thus, although this hypothesis is quite intriguing there is yet very little physiological evidence to explain the mechanisms of how such internal kinematic and dynamic limb models may be built.

E. Equilibrium Point Hypothesis

An alternative hypothesis which circumvents the problems associated with complex computations and accurate estimates of inertial parameters, has been formulated on the basis of the spring like behaviour of muscles in which movement dynamics are not explicitly considered.

(i). Lambda or Mass spring model

Feldman first proposed the mass-spring model (1966) in which agonist-antagonist muscles are represented by a pair of springs acting across a joint, against the mass of the segment. The position of the limb at rest will depend on the tension in the opposing springs. This tension in turn varies with the resting length. Thus, the load and the muscle characteristics interact to produce a point where the limb is in equilibrium. In order for movement to occur, the nervous system changes the extent of muscle activation which changes the length-tension properties of the opposing muscles, resulting in a shift in the equilibrium point of the muscle-load system. These changes are thought to be mediated by the tonic stretch reflex. In this model movement is considered to be a step change from one position of static equilibrium to another. As such, the movement trajectory is not controlled and the final position is achieved independently of initial conditions and movement dynamics.

Experiments on vestibulectomized and deafferented monkeys showed that final target position was achieved in spite of the application of unexpected loads (Bizzi et al, 1976; Polit and Bizzi, 1979). These and other experiments (Kelso and Holt, 1980) suggested that proprioceptive information was not necessary to achieve final position and that the CNS controls single joint movements simply by specifying the final equilibrium point. However, other studies have found errors in movement end point, following application of viscous loads in interphalangeal movements where the thumb was anaesthetized (Day and Marsden, 1982) as well as during unexpected perturbations of small amplitude movements (Sanes and Evarts, 1983). These findings which suggest the importance of sensory feedback on movement accuracy have led to modifications of the original equilibrium point hypothesis by different investigators.

(ii). Alpha model

Bizzi and his colleagues (1984) modified the mass-spring model and proposed the alpha model based on more recent work in monkeys. In these studies the monkey's forearm was briefly held in initial position after the final position target has been presented. After the forearm was released, the initial acceleration increased gradually with the duration of the holding period. Furthermore, by displacing the arm during the movement, they observed that following application of an assisting torque pulse, the arm did not return to the initial or final position but to intermediate points before moving to the end point. The authors suggested therefore that the CNS controls the trajectory of the arm by specifying a series of equilibrium positions throughout the movement. Specifically the time sequence of commands would give rise to a sequence of moving equilibrium points or a virtual trajectory (Bizzi et al, 1992). Furthermore since results of these experiments were found to be qualitatively similar between normal and deafferented monkeys this suggested that sensory feedback was unnecessary for movement.

F. Summary

The validity of the equilibrium point model is presently a hotly debated issue in motor control. One significant point of contention is that the model does not sufficiently account for the role of sensory feedback information in the control of movement. This is a serious weakness considering the plethora of evidence indicating that feedback from muscle, joint, cutaneous afferent (see Gandevia and Burke for review, 1992) as well as visual feedback (see Jeannerod, 1988) is essential for movement control. Although the virtue of the model is espoused on the basis of its computational simplicity (Bizzi et al, 1992), the model has been unable to adequately account for the generation of fast movements (see Bizzi et al, 1992) as well as multi-joint movements.

There have in fact been several recent attempts to apply the equilibrium point hypothesis to the control of multijoint movements. The basic premise of these approaches is that reaching is planned in terms of the equilibrium point of the hand, i.e. that desired hand trajectories are transformed into hand equilibrium trajectories (Flash, 1987; Flanagan et al, 1993). The joint torque profiles are then automatically generated as a result of the mechanical properties of the muscle, thus obviating the need to solve the inverse dynamic problem (Flash, 1990). Thus far there appears to be a good correspondence between the predicted and actual hand trajectories based on this model (Flash, 1990; Flanagan et al, 1993).

The current competing hypothesis, based on solving the inverse kinematic and dynamic problem, has been criticized on the basis of the need for precise calculations for the production of accurate movements. However, Cordo and Bevan (1992) have proposed that such precision may only be necessary in conditions where no sensory information is available to guide the movement. Given that normal movements are modulated by sensory feedback, the initial movement may be generated by approximating limb parameters. Sensory information can then by utilized to make adjustments during the movement. It would appear that the role of sensory information may be critical to the future development of models of movement control.

1.5 Summary

The above brief review has summarized the historical development of the study of upper limb control from two different levels of analysis: kinematic/kinetic and global muscle activity. Traditional approaches had for many years, focused on analysis of movement kinematics and the underlying muscle activity during movements about a single joint. This approach has provided the foundation for further study of multi-joint movements of which much remains to be learned.

One of the goals of the present research was to establish whether invariant relationships exist between planning of simple planar, single joint movements and more complex movements. Although there has been much controversy in the literature regarding the applicability of single joint studies in facilitating understanding of multi-joint movements, so far there has been no systematic attempts to discern any link between these two types of movement. In this respect, as a first step, the effects of gravitational loading in single joint movements were compared to findings from single joint movements made in the horizontal plane. In this experiment the EMG-movement relations were examined with the objective of determining consistent relationships under both conditions.

The purpose of the second and third set of experiments was to study the selection and pattern of muscle activity in planar two-joint movements. In each, the influence of elbow rotation on wrist movement was studied by manipulating the direction of movement of the two joints. A detailed analysis was conducted in which kinematics, and dynamics were correlated with muscle activity to evaluate the influence of various torques on the resulting movement and to ascertain possible mechanisms for generating movement.

In the last experiment, the characteristics of visual feedback information on inter-joint coordination were studied in two-joint planar movements. The visual displays ranged from concrete to abstract representations of the endpoint targets as well as the subject's arm position. Timing relationships between the joints as well as EMG activity under each condition were studied. The relevance of these studies to current understanding of upper limb coordination is discussed.

EFFECTS OF GRAVITATIONAL LOADING ON SINGLE JOINT ARM MOVEMENTS

2.1 Introduction

A major focus of research in motor control has been directed towards describing the relationship between specific kinematic variables and the underlying muscle activation patterns in order to identify regularities in the coordination of limb movement. To this end, many studies in the past have been restricted to single joint movements in the horizontal plane. Such movements, however, comprise only a small part of our "natural" movement repertoire. Many movements are made in the vertical plane where a number of complexities arise due to the influence of gravitational forces. For example, the magnitude of the gravitational torque does not remain constant but changes with joint angle. Furthermore, gravitational loads pose different demands for the motor system depending on the direction in which the movement is made, i.e. elbow flexions are commonly made against gravity, while elbow extensions are made with gravity. How does the CNS organize such movements and how does this organization compare or relate to the known properties of movements made in the horizontal plane?

To date, few studies have examined both the kinematics and the underlying muscle activation patterns for movements in the vertical plane. The purpose of this study was to examine and compare the EMG-movement relationships in single joint movements, made in both the horizontal and vertical planes.

2.2 Methods

A. Experimental Paradigm

Eight normal subjects (aged 22-52) with no known history of motor system disorders participated in this study. Subjects performed elbow flexion and extension movements in a visual step-tracking paradigm. The subject's forearm position was displayed as a horizontal line on a television monitor, placed at eye level 1.8m in front of the subject. A horizontal target bar displayed on the screen switched at a regular rate (every 5 sec) between two fixed vertical positions. Movement of the arm upwards produced an upward movement of the cursor; similarly, downward movement of the arm produced a downward movement of the cursor. Subjects were required to superimpose the position cursor on the target bar and were instructed to move "fast and accurately." By adjusting the shoulder position, elbow flexion and extension movements were made under the following three conditions:

i) Vertical plane: flexion against gravity/extension with gravity

Each subject was seated comfortably with the shoulder in 0 deg abduction, elbow flexed to 100 deg (full elbow extension = 180 deg), forearm supinated and fingers lightly flexed. Movements of five different amplitudes (5,10,20,30, and 40 deg) were performed from this starting position. At each amplitude a block of 30 movements consisting of 15 flexion and 15 extension movements was performed. Presentation of each new block was preceded by a rest period of 2-3 minutes. Several practice movements were made at each amplitude prior to data collection.

ii) Vertical plane: flexion with gravity/extension against gravity

In three subjects the direction of the gravitational load was reversed. Each subject was seated with the shoulder flexed to 180 deg, elbow flexed to 100 deg, forearm supinated and fingers lightly flexed. In this position 30 deg elbow flexion movements were made with gravity while extension movements were made against gravity. Each experimental session consisted of two blocks of movements, each block consisting of a total of 15 movements (8 flexion and 7 extension). The number of trials in each block was reduced in this condition in order to reduce fatigue resulting from maintaining the shoulder in this position for prolonged periods of time. The same three subjects also performed 30 deg elbow flexion movements against gravity and extension movements with gravity.

iii) Horizontal plane

Each subject was seated comfortably and grasped a vertical rod attached to a manipulandum which rotated in the horizontal plane about a vertical axis. The subject's shoulder was abducted to 90 deg with the elbow flexed to 100 deg and supported beneath the pivot point. Thirty elbow movements at an amplitude of 20 degrees were performed in this position.

Six subjects performed all the movements outlined under conditions one and three. Movements from both conditions were recorded during the same session. Movements in condition two were recorded from one of the initial six subjects plus an additional two subjects.

B. Data Recording

Angular positions for movements made in the vertical plane were obtained using an electrogoniometer (Penny and Giles). For movements in the horizontal plane, the angular position of the manipulandum (and thus the elbow joint) was measured with a precision potentiometer. Surface EMGs were recorded from the biceps and lateral head of triceps brachii with Ag-AgCl electrodes (.8 cm in diameter) placed longitudinally about 3 cm apart over the muscle bellies. EMGs were filtered (10 to 1000 Hz bandpass) and full wave rectified prior to digitization. The data were digitized online at 500 Hz, and stored for later off-line analysis.

C. Data Analysis

Kinematic data were smoothed by digital filtering (30 Hz, zero phase shift) prior to analysis. Velocity and acceleration were obtained from individual flexion and extension movements by differentiation of the position signal. The times of the start and end of acceleration and deceleration were determined using a threshold of 120 deg/sec^2. These times were used in determining movement duration, peak velocity and symmetry ratio (i.e the ratio of acceleration duration to deceleration duration). Mean values for peak velocity, movement duration and acceleration/deceleration duration ratios from each subject were used to calculate the means and standard deviations across all subjects, at each amplitude. Onset and offset times of EMG bursts were determined using interactive graphics. Only those records in which EMG onset and offsets could be clearly identified were used for analysis. As a result records from only three subjects were used for this analysis.

D. Moments of force

Since the EMG activity must, in some way, reflect the force output of the muscles, the torques acting on the limb were analyzed using the following equation governing the motion of a single segment (see appendix 4 for force diagram and Winter (1991) for more details):

$$I\alpha = T_m - mgr\cos\theta$$

where:

$I = I_o + mr^2$ (*where* I_o = *moment of inertia about center of mass*)

α = *angular acceleration* (rad/s^2)

T_m = *moment of force (torque) due to muscle activity*

m = *mass of the segment (forearm plus hand)*

g = *gravitational acceleration*

r = *distance from center of mass to the center of rotation*

θ = *segment angle* (rad)

This equation can also be written as:

$$T_e = T_m - T_g$$

where:

T_e = *net torque resulting in angular acceleration of the limb*

T_m = *torque due to muscle activity*

T_g = *torque due to gravitational acceleration*

2.3 Results

A. Movement Kinematics

Averaged position and velocity records of extension (with gravity) and flexion (against gravity) movements made in the vertical plane by one representative subject are shown in Fig. 1. The characteristic bell shaped velocity profile was observed at all amplitudes for both flexion and extension movements. In several subjects, extension movements made with gravity did not terminate smoothly and a small period of oscillation was observed at the end of movement. In flexion movements, this was only observed in large amplitude movements.

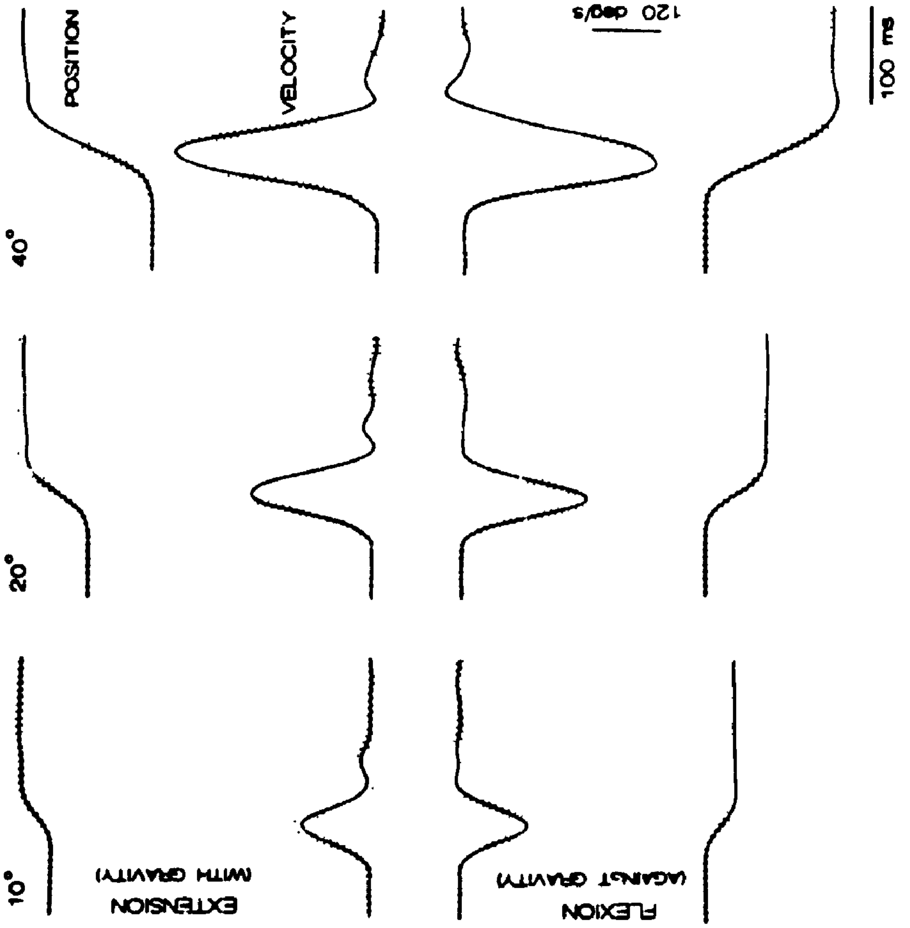
Changes in kinematic parameters with movement amplitude for flexions against gravity and extensions with gravity across six subjects are shown in Fig. 2. Peak velocity increased linearly with movement amplitude for both flexion ($r = .99$) and extension ($r = .99$) movements (Fig. 2A). There was no significant difference in the slopes ($p = .15$). In addition, no significant difference was found in the peak velocities between flexions and extensions at any amplitude (e.g. for 40 deg amp: $p = .43$). Fig. 2B illustrates the relation between movement duration and movement amplitude. Movement duration increased linearly with movement amplitude for both flexion and extension (flexion: $r = 0.97$; extension: $r = 0.96$). On average, extension (with gravity) movements appeared to be of shorter duration than flexion (against gravity) movements. However, no significant differences were found between the slopes ($p = .37$) or between movement durations at any amplitude (for 40 deg amp: $p = .23$).

Mean symmetry ratios (acceleration duration/deceleration duration) are plotted in Fig. 2C for six subjects. A significant difference was found between the slopes of the two regression lines ($p < .05$). For flexion movements there was a trend towards decreasing symmetry ratios as amplitude increased. Symmetry ratios ranged from 0.8 to 0.9 with a mean of 0.82 indicating that on average, the duration of deceleration was slightly greater than the duration of acceleration for movements made against gravity. Extension movements made with gravity exhibited a trend towards increasing symmetry ratios as amplitude increased. Symmetry ratios ranged from 0.8 - 1.2, with a mean of 0.9. Statistical analysis, however, revealed a significant difference only for 30 degree movements ($p = .006$). This difference may have arisen in part from the data of one particular subject who had consistently larger symmetry ratios for extension and smaller ratios for flexions at the larger amplitudes. If this subject's data were removed, no significant differences remained. In general extension movements were time symmetric at all amplitudes. Flexion movements exhibited slightly asymmetric profiles with deceleration duration marginally greater than acceleration duration.

In order to further compare flexion and extension movement profiles, averaged velocity records were adjusted for movement duration and peak velocity. Averaged flexion records for each amplitude were used as a reference. The averaged peak velocities and movement durations from extension movements were scaled by an appropriate factor and overplotted on the flexion records. Fig. 3 illustrates the velocity profiles from one subject. This figure illustrates an overlap in the velocity

Figure 1

Movements made with and against gravity. Records of position and velocity from extension (with gravity - upper set) and flexion (against gravity - lower set) are shown for movements of three amplitudes (10, 20, and 40 deg). Each record is the average of 15 movements. Dashed lines indicate +/- 1 SD. Records were aligned to movement start for averaging.


10°
20°
40°
POSITION
VELOCITY
120 deg/s
100 ms
EXTENSION (WITH GRAVITY)
FLEXION (AGAINST GRAVITY)

profiles between the two different movements at all amplitudes, demonstrating that a common movement profile was produced for movements with and against gravity.

B. Muscle activation patterns/Moments of Force

(i) Horizontal Plane

In Fig. 4 the averaged position, velocity and associated EMGs are shown for flexion and extension movements made in the horizontal plane. Both flexion and extension movements were time-symmetric and in both, AG1 occurred prior to movement start, providing the driving force to set the limb in motion. Phasic activity in ANT occurred at or near peak velocity and was followed by a second, smaller burst in the agonist (AG2).

(ii) Vertical Plane: Flexion against gravity/extension with gravity

The muscle activation patterns associated with flexion (upper panel) and extension (lower panel) movements made in the vertical plane are illustrated in Fig. 5. Both flexion and extension movements were initiated by AG1 which occurred prior to movement start. The data from this subject shows that AG1 occurred earlier (with respect to movement onset) for movements made with gravity, in comparison to movements made against gravity; this was not however, a consistent finding across all subjects. The most striking difference between flexion and extension movements was related to the time of onset of phasic antagonist activity. For flexion movements made against gravity, phasic antagonist activity started at virtually the same time as AG1. A second antagonist burst followed at about the time of movement peak velocity. In contrast, in extension movements made with gravity, a single antagonist

Figure 2

Kinematic relations. Graphs of peak velocity (A), movement duration (B) and the ratio of acceleration to deceleration durations (C) are shown for flexions against gravity and extensions with gravity. Each point is the average (+/- 1SD) obtained from 6 subjects. Solid lines are the best-fit linear regression lines for data from flexions (closed symbols) and extensions (open symbols). (A) Peak velocity/amplitude -flexion: Vp = 45 + 5.9A; extension: Vp = 44 + 6.5A. (B) Movement duration/amplitude - flexion: MD = 196 + 3.1A, r = 0.97; extension: MD = 177 + 2.9A, r = 0.96. (C) Symmetry ratio/amplitude -flexion: SR = 0.88 - 0.003A, r = 0.71; extension: SR = 0.86+ 0.004A, r = 0.76) The dashed horizontal line in (C) indicates a ratio of 1.0.

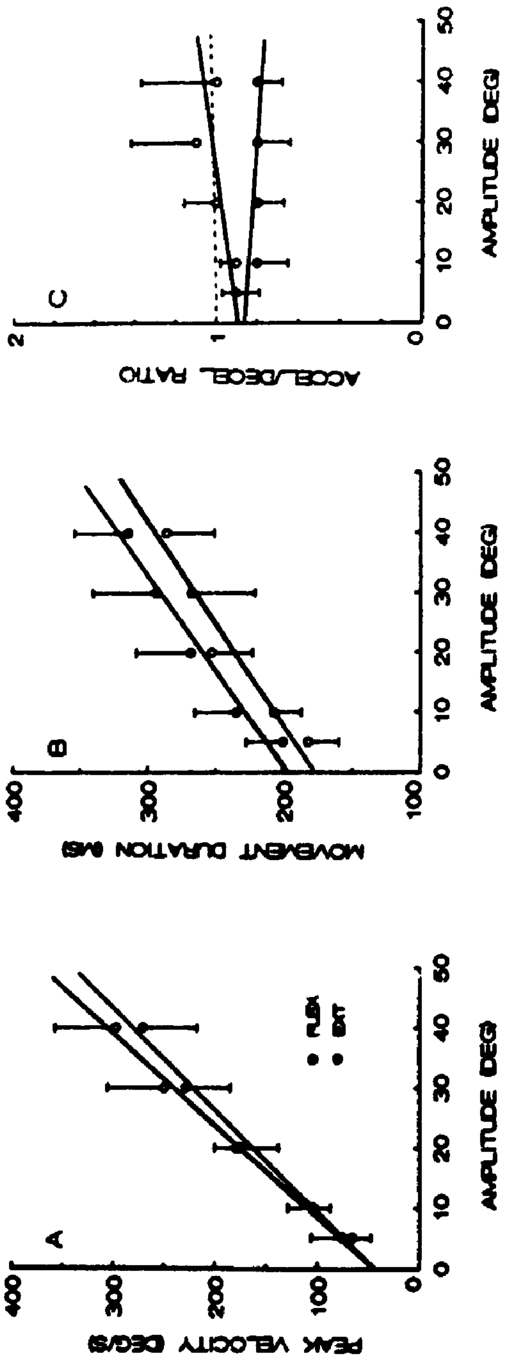
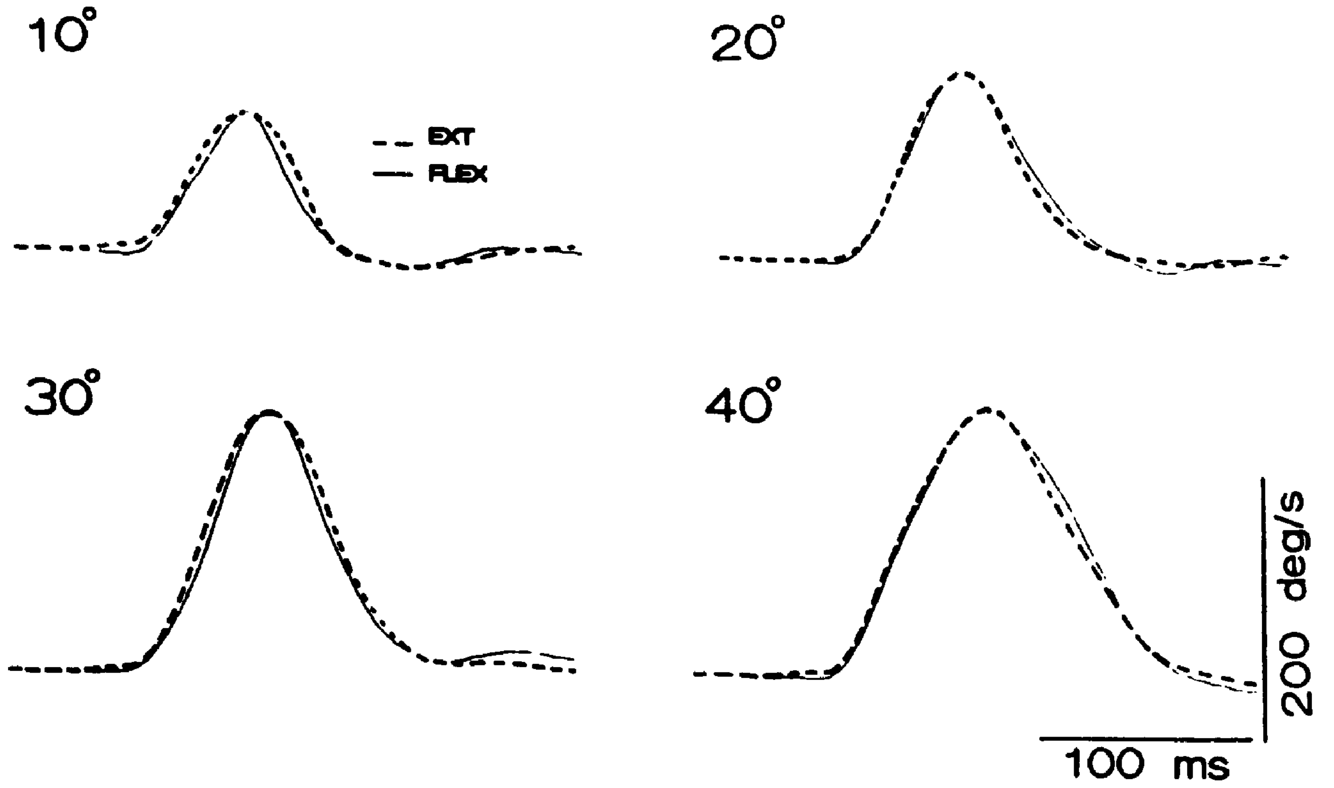

A
B
C
PEAK VELOCITY (DEG/S)
MOVEMENT DURATION (MS)
ACCEL/DECEL RATIO
AMPLITUDE (DEG)
FLEX
EXT
0
100
200
300
400
2
1
10
20
30
40
50

Figure 3

Scaling of velocity profiles. Averaged velocity records are shown from movements of four amplitudes (10, 20, 30 and 40 deg) made by one subject. Each record is the average of 15 movements. At each movement amplitude, the average velocity records from extension movements (dashed lines) were scaled to the duration and peak velocity of the corresponding flexion movements (solid lines) and inverted for plotting. Records were aligned to movement onset for averaging and plotting.


10°
EXT
FLEX
20°
30°
40°
200 deg/s
100 ms

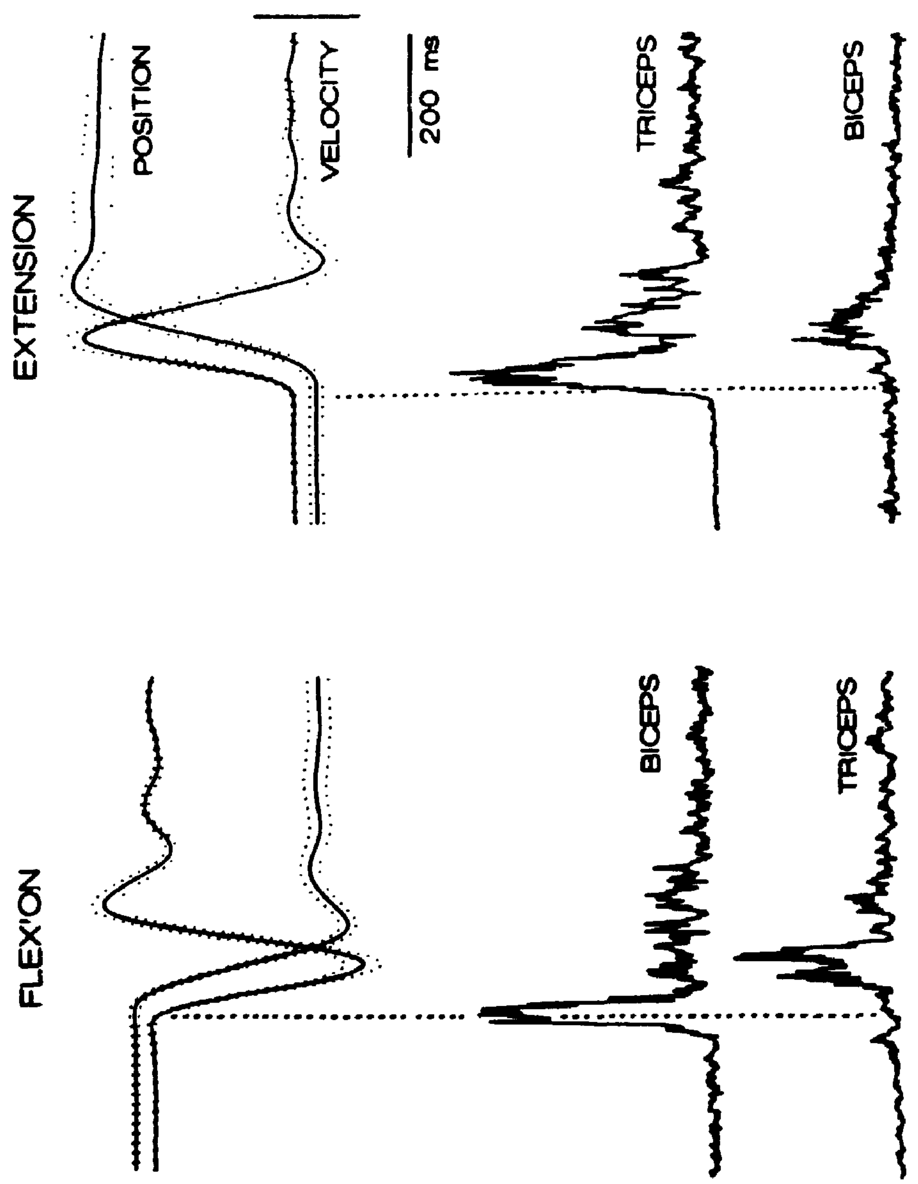
burst occurred later in the movement, near the time of peak velocity.

A linear relationship was observed between AG1 duration and movement amplitude in both flexion and extension movements. However, differences were observed in the slopes of this relation. The data in Fig. 6 represent averaged burst durations taken from individual records from three subjects. For flexion (against gravity) movements the mean burst durations ranged from 57 (+/-1) ms for 10 deg movements to 112 (+/-3) ms for 40 deg movements. For extension (with gravity) movements burst durations ranged from 48 (+/-9) ms for 10 deg movements to 62 (+/-11) ms for 40 deg movements. Although in both flexion and extension movements AG1 duration increased linearly with movement amplitude (flexion: $r = 0.99$; extension: $r = 0.92$), the slope of the relation was greater in flexion movements. A significant difference was found between the slopes of the two regression lines ($p < .001$). The right hand graph in Fig. 6 shows the time of onset of (ANT) relative to the onset of (AG1), for both flexion (against gravity) and extension (with gravity) movements. In flexions, ANT onset occurred on the average, 12 (+/- 4.6) ms after the onset of AG1. Since the shortest agonist burst duration was 57 (+/-1) ms, this indicates that phasic activity in the agonist and antagonist occurred quite close together. In contrast, during extension movements, ANT onset occurred on the average, 91.5 (+/-22.5) ms after the onset of AG1. The largest mean AG1 burst duration in this case was 62 (+/-11) ms. Thus, there was little if any AG1-ANT coactivity during extension movements.

Fig. 7 shows the torques due to gravity (T_g), muscle activity (T_m) and the net

Figure 4

EMG activity during single joint elbow flexion and extension movements made in the horizontal plane. Averaged position and velocity records from flexion and extension movements in the horizontal plane. Records are the average of 15 movements for 20 deg movements. Records were aligned to movement start for averaging. Dotted line indicates movement onset. Vertical position and velocity calibration represents 10 deg and 130 deg/sec respectively.

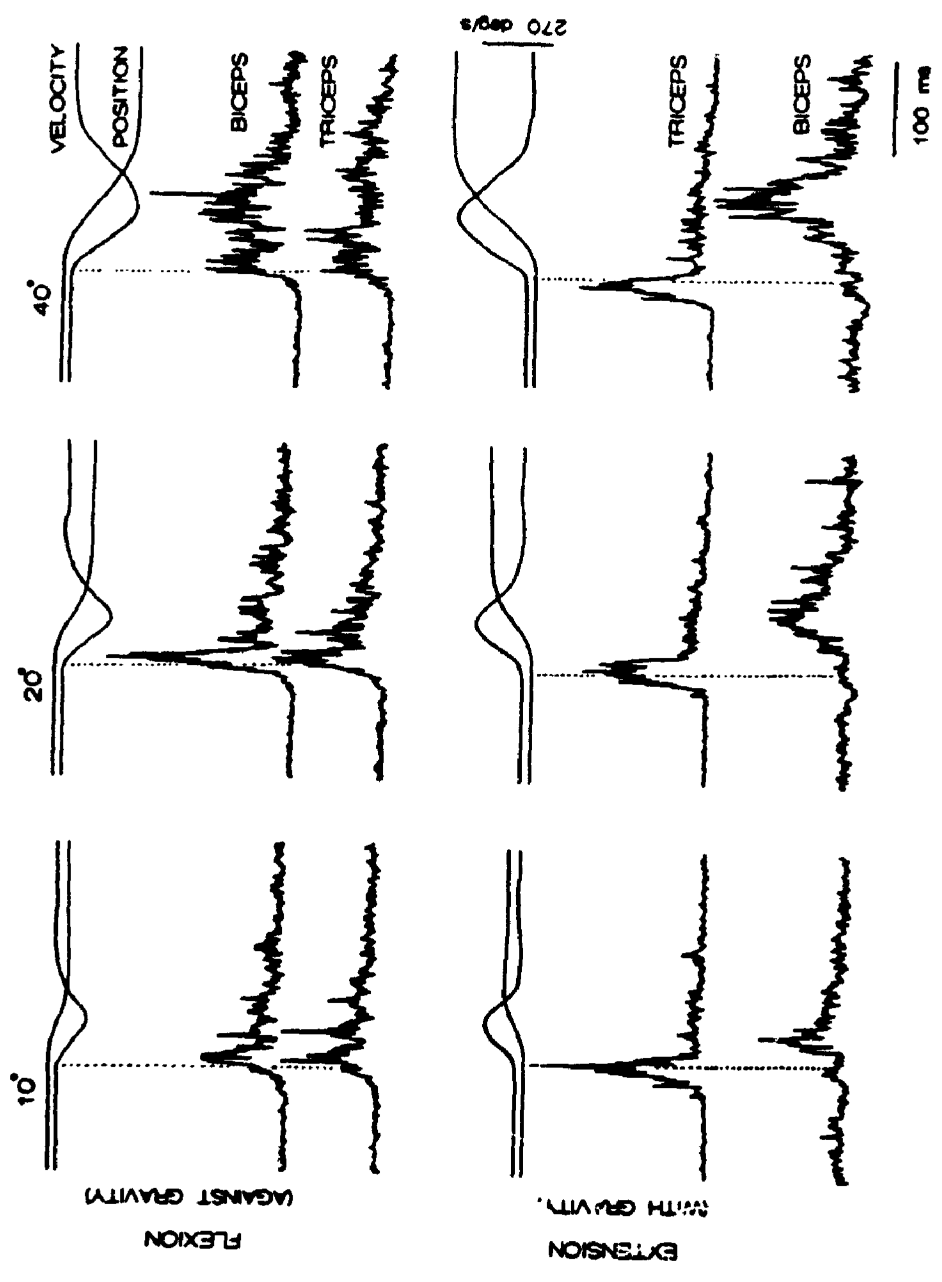


FLEXION
BICEPS
TRICEPS
EXTENSION
POSITION
VELOCITY
200 ms
TRICEPS
BICEPS

torque (T_t) calculated from the averaged data of one representative subject for a movement amplitude of 30 deg. By convention, forearm movement in a counterclockwise direction (flexion) was considered to be positive and those in a clockwise direction (extension), negative. In both flexion (against gravity) and extension (with gravity) movements, the magnitude of the static torque (prior to movement start) due to gravity (T_g) was approximately 1.7 Nm, acting in a negative direction to produce a clockwise rotation of the forearm. Note that there was little change in the magnitude of T_g throughout both flexion and extension movements. In flexion (against gravity) movements, T_g was acting in a direction opposite to the intended movement (Fig. 8 -left of panel). The magnitude of T_m was 1.7 Nm prior to movement start and increased to 2.7 Nm at the time of peak torque. The net change in magnitude and direction of T_m was due to two distinct components. The first was the change in torque needed to overcome the inertial forces: this was proportional to acceleration. The second was the flexor torque required to compensate for T_g. Since there was little change in the magnitude of T_g during the movement, the component of T_m necessary to overcome T_g was held approximately constant as movement progressed. That is, the presence of T_g served to increase the baseline magnitude of T_m. The right panel in Fig. 8 illustrates that in flexion movements made with gravity, T_g was acting in the same direction as the intended limb movement. The magnitude of T_m was 1.5 Nm prior to movement start and decreased to 0.7 Nm at the time of peak torque. Again, the magnitude and direction of T_m was based on the torque necessary to overcome the inertial forces and to

Figure 5

EMG activity during elbow movements made in the vertical plane. In each set of records are shown averaged position, velocity and EMG activity for movements of three amplitudes (10, 20, and 40 deg). Traces are the average of 15 movements. The upper set illustrates flexion (against gravity) movements and the lower set illustrates extension (with gravity) movements. Records were aligned to movement start for averaging. Vertical dotted line indicates movement onset. It should be noted that the amplitude scale across all panels is constant.

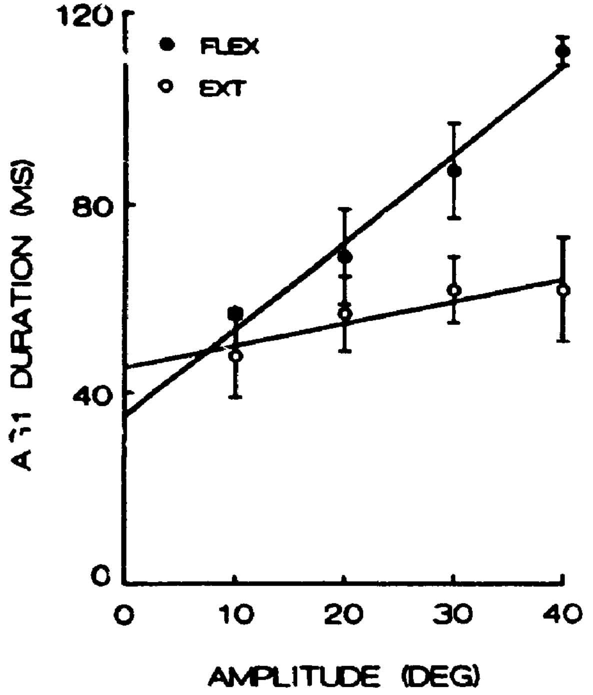

FLEXION
(AGAINST GRAVITY)
EXTENSION
(WITH GRAVITY)
10°
20°
40°
VELOCITY
POSITION
BICEPS
TRICEPS
270 deg/s
TRICEPS
BICEPS
100 ms

account for the presence of T_g. In this case, however, T_g served to assist limb acceleration, resulting in a decrease in the magnitude of T_m as the movement progressed. As illustrated, an increase in flexor torque was required to overcome the clockwise torque due to T_g and bring the limb to a stop.

The reversal in the pattern of the gravitational load resulted in an appropriate modulation of the muscle activation patterns. Fig. 8 illustrates the averaged position and velocity records and the torques due to gravity (T_g), muscle contraction (T_m) and net torque producing angular rotation (T_e) for flexion (with gravity) and extension (against gravity) movements. The corresponding averaged EMG muscle activation patterns are also shown. In this task T_g was acting to produce a positive or counterclockwise rotation of the forearm. Thus, in flexion movements made with gravity, T_g was acting in the same direction as the limb movement (right hand graph in Fig. 8). A static flexor torque of -1.4 Nm was produced prior to movement start and decreased to -0.8 Nm at the time of peak force. In extension (against gravity) movements, T_g was acting in a direction opposite to the intended movement. A static extensor torque of -1.4 Nm was produced prior to movement start and increased to -2.5 Nm at the time of peak acceleration. Flexion movements made with gravity exhibited an initial agonist burst followed by phasic activity in the antagonist, similar to that previously observed in extension movements performed with gravity. Extension movements made against gravity showed early, simultaneous phasic muscle activity in both the agonist and antagonist, as had been observed in flexion movements against gravity.

Figure 6

AG1 Duration and onset latency of ANT. The change in AG1 duration with amplitude is shown in the left hand graph. Each point is the average (+/- 1SD) obtained from 3 subjects. Solid lines are the best-fit linear regression lines for data from flexions (closed symbols) and extensions (open symbols). The right hand graph shows the time span between the onset of AG1 and ANT. Each bar is the average (+/- 1SD) from 3 subjects. Flexions are indicated by open bars and extensions by striped bars


120
80
40
0
AG1 DURATION (MS)
● FLEX
○ EXT
0
10
20
30
40
AMPLITUDE (DEG)

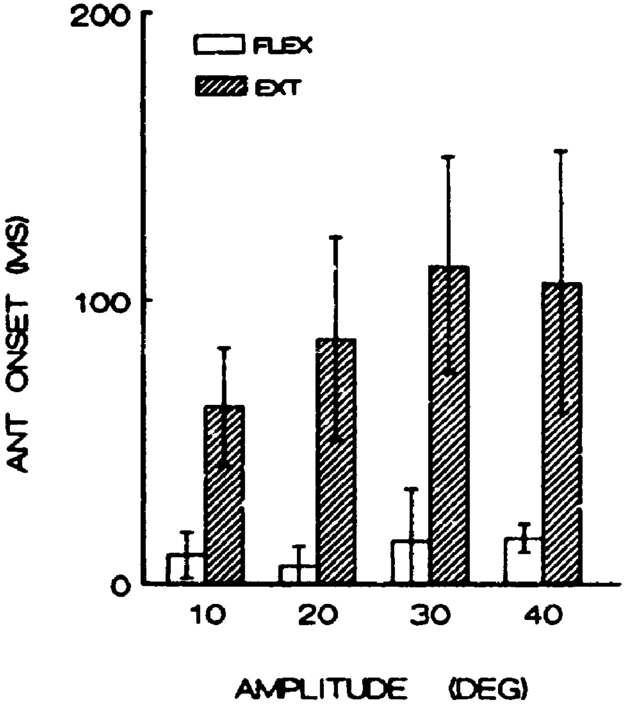

200
100
0
ANT ONSET (MS)
☐ FLEX
▨ EXT
10
20
30
40
AMPLITUDE (DEG)

Figure 7

Calculated torques during movement. Records of the torque due to gravity *(T_g)*, torque due to muscle activity *(T_m)* and net torque *(T_e)* for flexion (against gravity) and extension (with gravity) movements. Traces are the average of 10 movements for 30 deg movements.

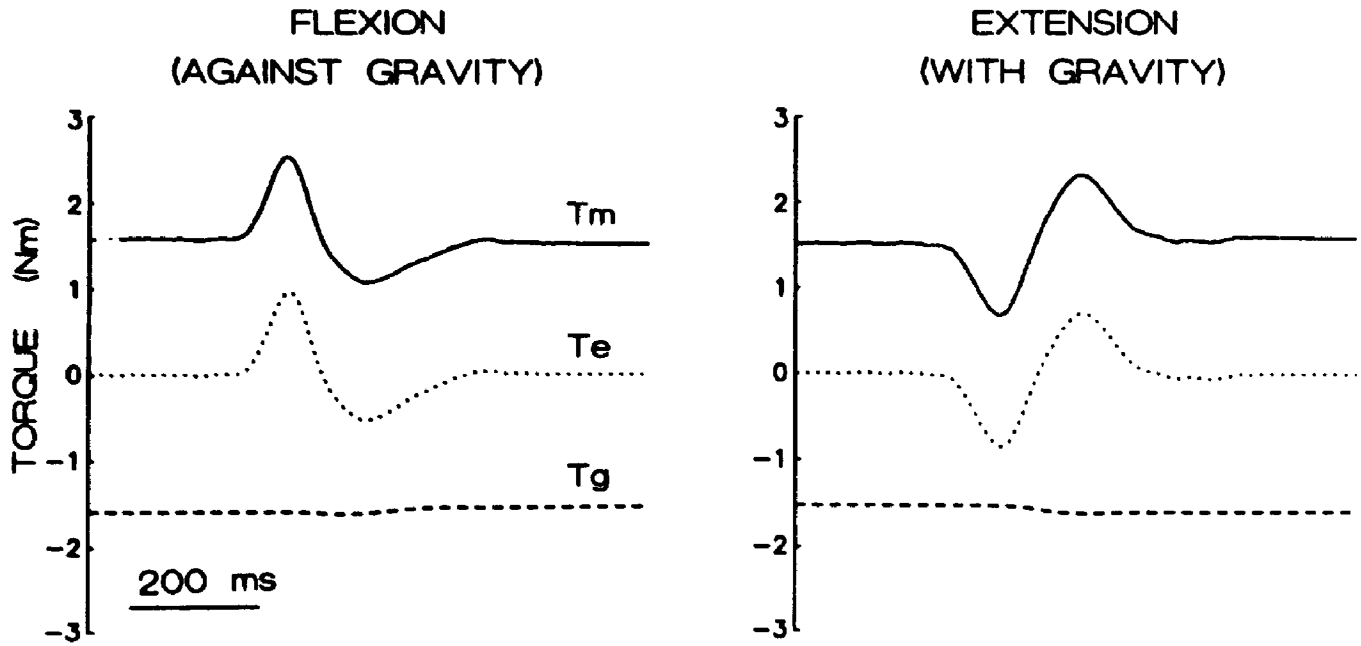
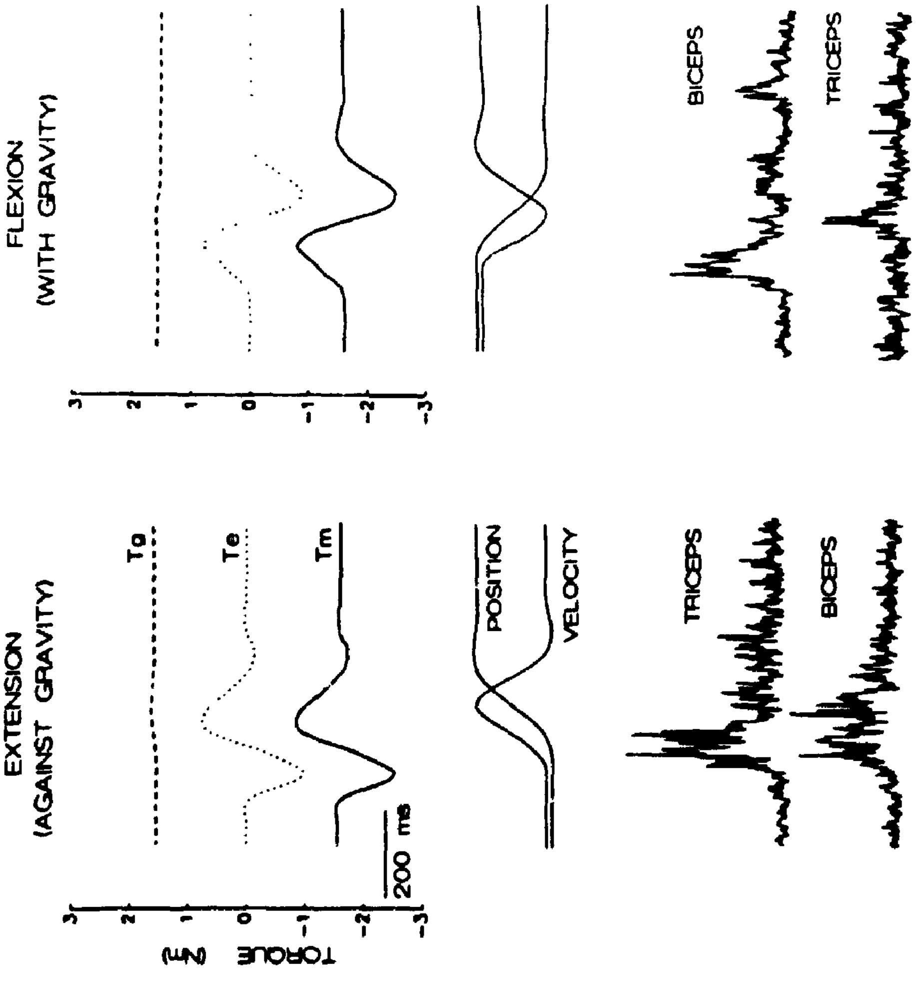

FLEXION
(AGAINST GRAVITY)
EXTENSION
(WITH GRAVITY)
TORQUE (Nm)
3
2
1
0
−1
−2
−3
Tm
Te
Tg
200 ms
3
2
1
0
−1
−2
−3

Figure 8

Torques and EMGs during reversed loading conditions. Records of the torque due to gravity (T_g), torque due to muscle activity (T_m) and net torque (T_i) for flexion (with gravity) and extension (against gravity) movements. In each set of records are shown the averaged position, velocity and EMG activity for 30 deg movements. Traces are the average of 10 movements. Records were aligned to movement start for averaging.


EXTENSION
(AGAINST GRAVITY)
FLEXION
(WITH GRAVITY)
TORQUE (Nm)
3
2
1
0
-1
-2
-3
Ta
Te
Tm
200 ms
POSITION
VELOCITY
TRICEPS
BICEPS
BICEPS
TRICEPS

2.4 Summary

The results of this study have demonstrated that simply by introducing one additional level of complexity (i.e. gravitational loading), the known relationships between phasic muscle activity and particular kinematic variables were modified with respect to the task conditions. For example, although movements made with and against gravity were both characterized by time symmetric velocity profiles, the associated patterns of muscle activity were quite different and specific for each condition. Furthermore, significant differences were apparent in the relationship between AG1 duration and movement amplitude in movements made with and against gravity. Across a 30 degree range of movement amplitude, AG1 duration increased by 96% in movements made against gravity. This finding is similar to that reported for movements made in the horizontal plane (Berardelli et al, 1984; Brown and Cooke, 1984). In contrast, AG1 burst duration increased by only 29% in movements made with gravity, across the same amplitude.

These modifications appear to be directly influenced by the gravitational torque. During extension movements, the torque due to gravitational acceleration acted in the same direction as the movement. Hence, it is quite possible that the CNS takes advantage of gravitational forces and uses it in *combination* with muscle activity to produce such movements. This would then result in a reduction of the total muscle activity required to accelerate the limb, leading to a relatively small increase in AG1 duration with movement amplitude, compared to movements made against gravity or in the horizontal plane.

JOINT INTERACTIONAL EFFECTS ON THE COORDINATION OF PLANAR TWO-JOINT ARM MOVEMENTS IN THE SAME DIRECTION

3.1 Introduction

In searching for the strategies used by the CNS in controlling movement, the focus of study in recent years has shifted from analysis of single joint movements to multi-joint movements. It is now widely accepted that specific complexities arise during rotation about two or more joints (such as joint interactional effects resulting from reaction, centripetal and Coriolis torques) that are not present in the single joint case (Hollerbach and Flash, 1982). In order for coordinated movement to occur, it is generally assumed that the CNS must in some manner play an active role in counteracting the effects of interactional torques and in organizing the relationship between joint movement. Thus far however, few studies have directly examined the influence of such torques during multi-joint arm movements in addition to the kinematics and related muscle activation patterns (Karst and Hasan, 1991; Lacquaniti and Soechting 1982; Soechting and Lacquaniti 1981; Wadman et al, 1980). The purpose of this study was to examine the influence of interactional torques on movement coordination in two-joint planar movements during which both joints rotated in the same direction.

3.2 Methods

A. Experimental Paradigm

Six normal subjects (aged 23-38) with no known history of motor system disorders participated in this study. Subjects performed flexion and extension movements about the elbow and wrist joints in a step-tracking paradigm. A stick figure target composed of two connected bars, representing the forearm and hand, was displayed on a television monitor. The configuration of the two connected bars could be altered to independently set individual elbow and wrist angles. The subject's actual forearm and hand positions were displayed as two connected lines on the same monitor (see top insert in Fig. 18). The target stick figure switched at a regular rate (every 5 seconds) between the initial and final elbow and wrist positions. The subject's position was refreshed every 10 msec. Subjects were required to superimpose their forearm and hand positions on the target stick figure by moving the lines into the bar. The width of each bar corresponded to a movement amplitude of approximately 3 degrees. Subjects were instructed to move "fast and accurately" between the target bars. Movements that were off the target amplitude by greater than 5 degrees were discarded. This resulted in approximately 2-3% of the movements being discarded.

Subjects were seated comfortably and grasped a vertical rod attached to a biarticulated manipulandum which rotated in the horizontal plane about vertical axes at the elbow and wrist joints. Each subject's shoulder was abducted to 90 deg, with the forearm semi-prone. The forearm and the hand were supported along the length of the forearm and hand segments of the manipulandum. Subjects made alternate flexion and extension movements. The initial position for initiating movements was 35 degrees of elbow extension (0 deg equalling full extension) and 10 degrees of wrist extension for the hand. From this position subjects made elbow flexion/wrist flexion movements of various amplitudes, and returned to the initial position by making elbow extension/wrist extension movements. Subjects performed all movements with their dominant arm. Three target wrist amplitudes of 20, 30 and 40 deg were combined with three target elbow amplitudes of 20, 40 and 70 deg. This resulted in a total of 9 separate combinations of two-joint movement targets which were presented in a random order, in a single session. In all conditions both the elbow and wrist always rotated in the same direction, i.e. wrist flexion/elbow flexion and wrist extension/elbow extension. In each movement condition a block of 30 movements was performed consisting of 15 elbow flexion/wrist flexion and 15 elbow extension/wrist extension movements. Presentation of each new block was preceded by a rest period of 2-3 minutes. Approximately 10-20 practice movements were made at each condition prior to data collection.

B. Data Recording

The angular positions of the two joints were obtained using electrogoniometers (Penny and Giles). A crepe bandage was tied around each subject's forearm. The goniometers were attached to the surface of the bandage and then secured with adhesive tape. This ensured that there was minimal artifactual movement of the goniometers. Surface EMGs were recorded from biceps, lateral head of triceps, flexor carpi radialis and extensor carpi radialis with bipolar electrodes separated by 1 cm. All data were digitized on line (12 bit) at 500 Hz. EMGs were filtered (10 to 1000 Hz) and subsequently full wave rectified. The data were then stored for later off-line analysis.

C. Data Analysis

Velocity and acceleration were obtained from individual flexion and extension movements by digital differentiation of the position signal. The times of the start and end of acceleration and deceleration were determined using a threshold of 130 deg/s^2. These times were used in determining movement start, movement duration and peak velocity. Mean values for peak velocity and movement duration from each subject were used to calculate means and standard errors across all subjects. Onset times of AG1 bursts were determined using interactive graphics (Cooke and Brown, 1994). Only those records in which EMG onsets could be clearly determined were used for analysis.

The moment of inertia of each subject's forearm and hand segments were calculated from Dempster's estimates reported in Winter (1991). The following are the moments of inertia of the hand and forearm for one female subject: height: 1.6m; weight: 61 kg, I_1 (forearm) = .01 kg.m^2, I_2 (hand) = .001 kg.m^2. The moments of inertia of the manipulandum were estimated to be .006 kg.m^2 for the hand segment and .007 kg.m^2 for the forearm segment. The manipulandum was dismantled in order to obtain the weight of each segment. The muscle torques acting at the elbow (Tmm_1) and wrist (Tmm_2) joints were calculated using the following equations

(Hollerbach and Flash, 1982; Karst and Hasan, 1991): (See appendix 4 and 5)

$$Tmm_1 = [I_1 + I_2 + m_1 c_1^2 + m_2(l_1^2 + c_2^2 + 2 l_1 c_2 \cos\theta_2)]\alpha_1$$

$$+ (I_2 + m_2 c_2^2 + m_2 l_1 c_2 \cos\theta_2)\alpha_2$$

$$-(m_2 l_1 c_2 \sin\theta_2)\omega_2^2 - (2 m_2 l_1 c_2 \sin\theta_2)\omega_1\omega_2$$

$$Tmm_2 = (I_2 + m_2 c_2^2 + m_2 l_1 c_2 \cos\theta_2)\alpha_1 + (I_2 + m_2 c_2^2)\alpha_2 + (m_2 l_1 c_2 \sin\theta_2)\omega_1^2$$

where:

θ_1, θ_2 = *elbow, wrist joint angles respectively (rad)*

ω_1, ω_2 = *angular velocities (rad/s)*

α_1, α_2 = *angular accelerations (rad/s²)*

c_1, c_2 = *distance from the centre of mass to the proximal end of the segment*

I_1, I_2 = *the moments of inertia of the forearm and hand respectively about the centre of mass*

m_1, m_2 = *segment masses*

l_1, l_2 = *segment lengths*

The terms with angular velocity squared are the centripetal torques. For each joint the terms with the angular accelerations of the other joint are the reaction torques and the terms with the angular accelerations of the same joint are the net torques. For the wrist joint the equation can be written as:

$$T_{mm2} = T_{reaction} + T_{net} + T_{centripetal}$$

3.3 Results

A. Movement Kinematics

A sample of some of the different two-joint movement conditions used in this experiment are illustrated in Fig. 9. Averaged position and velocity records of elbow and wrist movements from one representative subject are shown. In Fig. 9A, wrist flexion movements of three different amplitudes (20, 30 and 40 deg) combined with elbow flexion of 20 deg are shown. Fig. 9B illustrates elbow extension movements of three different amplitudes (20, 40 and 70 deg) from the same subject, combined with wrist extension of 20 deg. In all conditions the wrist and elbow rotated in the same direction that is, flexion/flexion or extension/extension. Subjects performed both flexion and extension movements under all conditions. Note that the characteristic bell shaped velocity profile was observed at both joints in all conditions.

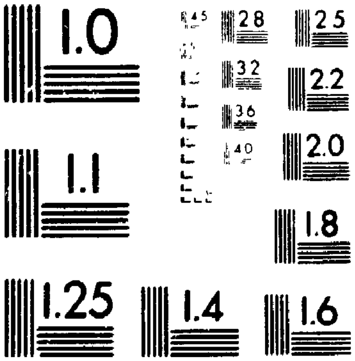
A qualitative examination of Fig. 9B shows that the kinematics of the wrist movements were influenced by concurrent elbow movements. The wrist peak velocity decreased and the wrist movement duration increased as the elbow amplitude increased. In contrast, the same figure (Fig. 9A) shows that the kinematics of the elbow movement were little affected by concurrent wrist movements. This was confirmed by plotting kinematic parameters of movements about one joint as a function of movement amplitude of the other joint. The relations of movement duration and peak velocity with movement amplitude across six subjects are shown in Fig. 10. Fig. 10A and B show data from elbow extension movements plotted as a function of *wrist* amplitude. Fig. 10A shows the change in elbow movement

Figure 9

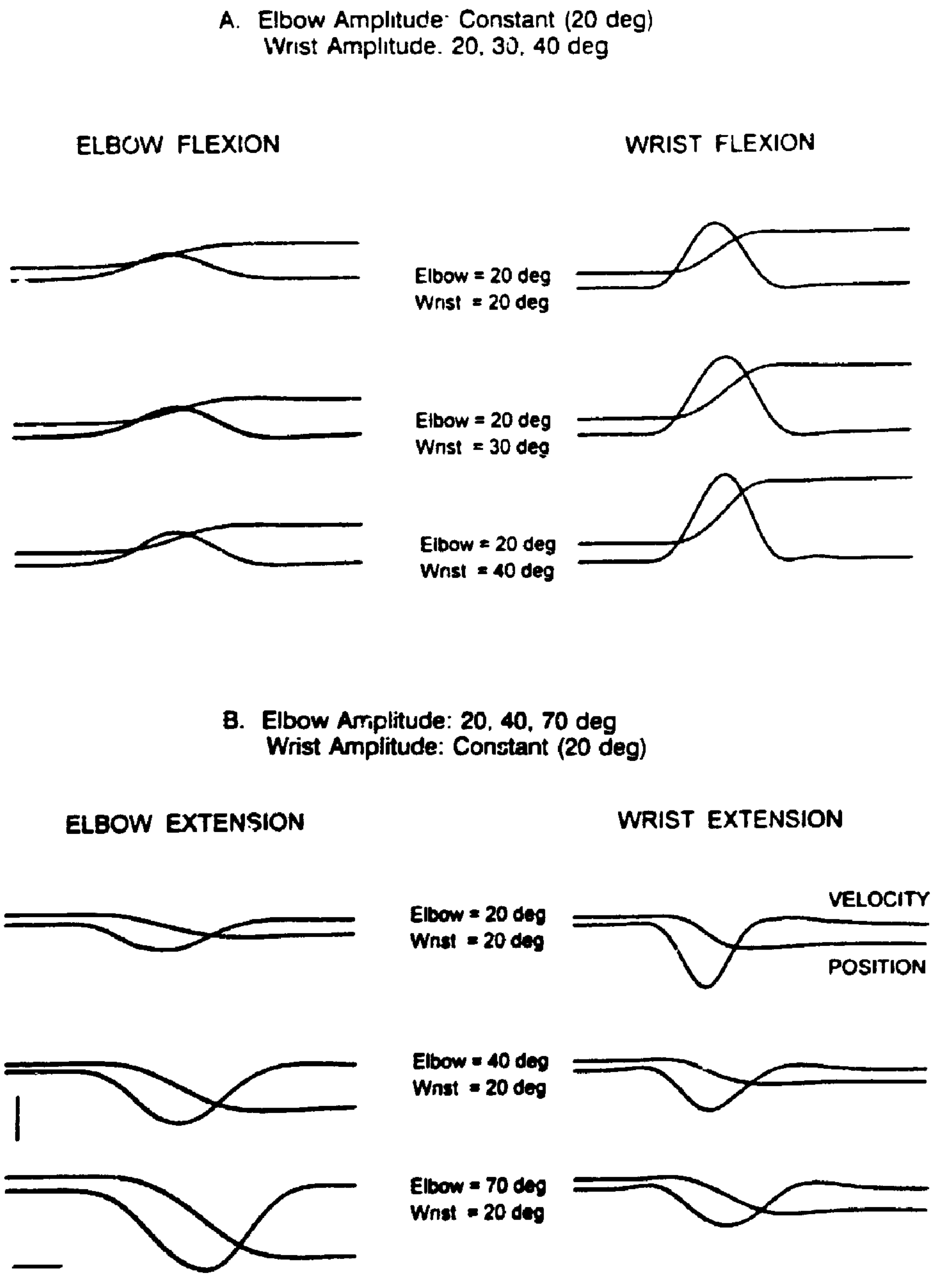
Two-joint elbow and wrist movements in the same direction. Records of position and velocity from combined flexion/flexion elbow and wrist movements (A) and combined extension/extension elbow and wrist movements (B) are shown. Each record is the average of 15 movements. Records were aligned to movement start for averaging. Vertical position and velocity calibration represents 30 deg and 130 deg/sec respectively. Horizontal calibration represents 100 ms.

2

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



PRECISION℠ RESOLUTION TARGETS

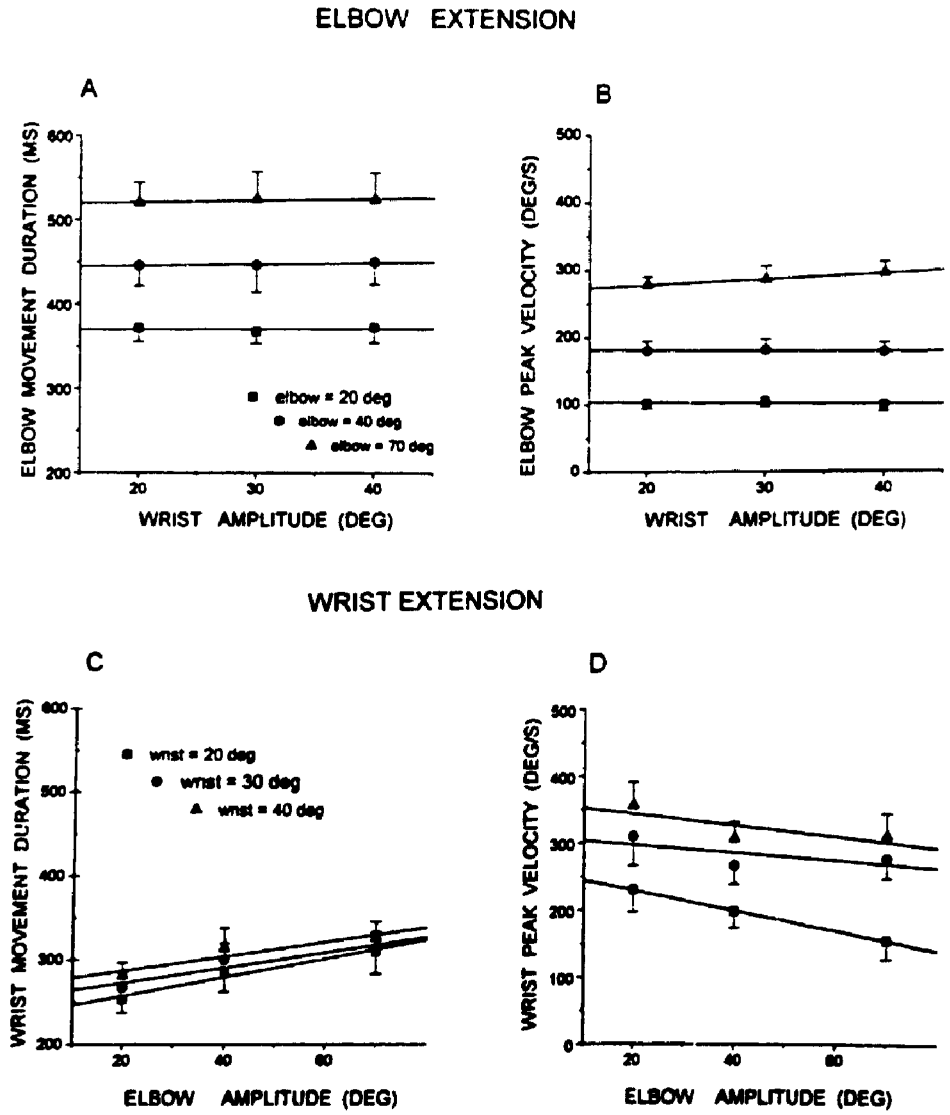

A. Elbow Amplitude: Constant (20 deg)
Wrist Amplitude. 20, 30, 40 deg
ELBOW FLEXION
WRIST FLEXION
Elbow = 20 deg
Wrist = 20 deg
Elbow = 20 deg
Wrist = 30 deg
Elbow = 20 deg
Wrist = 40 deg
B. Elbow Amplitude: 20, 40, 70 deg
Wrist Amplitude: Constant (20 deg)
ELBOW EXTENSION
WRIST EXTENSION
VELOCITY
POSITION
Elbow = 20 deg
Wrist = 20 deg
Elbow = 40 deg
Wrist = 20 deg
Elbow = 70 deg
Wrist = 20 deg

duration with wrist amplitude. There was very little change in the elbow movement duration with wrist amplitude (Fig 10A) as indicated by the slopes of the best fit linear regression lines (slopes ranged from 0.1 - 0.2 ms/deg). No significant differences were found between the slopes for different elbow amplitudes ($p>.6$). At each wrist amplitude, elbow movement duration increased significantly as elbow amplitude increased ($p< 0.03$). Fig. 10B illustrates the changes in elbow peak velocity with wrist amplitude. There was a small change in elbow peak velocity with wrist amplitude (slopes of the regression lines ranged from -0.2 to 0.8 ((deg/s)/deg). At all wrist amplitudes, elbow peak velocity increased significantly as elbow amplitude increased ($p< 0.0003$). Although not shown, similar relationships were observed for elbow flexion movements. Thus, elbow kinematics were not significantly influenced by motion of the wrist.

Fig. 10C shows wrist extension movement duration plotted as a function of *elbow* amplitude. A large increase was observed in wrist movement duration as elbow amplitude increased (slopes of the linear regression lines ranged from 0.9 to 1.1 ms/deg). There were no significant differences between the slopes at the different wrist amplitudes ($p>.7$) It should be noted that there were no significant differences in wrist movement durations as wrist movement amplitude increased, at any given elbow amplitude ($p > 0.1$). This is in contrast to the increase normally observed in movements about a single joint (Benecke et al, 1985; Brown and Cooke, 1984). Fig. 10D shows that at all wrist amplitudes, wrist peak velocity decreased with elbow amplitude (slopes ranged from -0.6 to -1.5 ((deg/s)/deg). There were no significant

Figure 10

Kinematic relations of one joint plotted as a function of the second joint. Graphs of elbow movement duration (A), elbow peak velocity (B), wrist movement duration (C) and wrist peak velocity (D) are shown. Each point is the average obtained from 6 subjects. Error bars are 1 SEM. Solid lines are the best-fit linear regression lines.


ELBOW EXTENSION
A
B
ELBOW MOVEMENT DURATION (MS)
600
500
400
300
200
elbow = 20 deg
elbow = 40 deg
elbow = 70 deg
20
30
40
WRIST AMPLITUDE (DEG)
ELBOW PEAK VELOCITY (DEG/S)
500
400
300
200
100
0
20
30
40
WRIST AMPLITUDE (DEG)
WRIST EXTENSION
C
D
WRIST MOVEMENT DURATION (MS)
600
500
400
300
200
wrist = 20 deg
wrist = 30 deg
wrist = 40 deg
20
40
60
ELBOW AMPLITUDE (DEG)
WRIST PEAK VELOCITY (DEG/S)
500
400
300
200
100
0
20
40
60
ELBOW AMPLITUDE (DEG)

difference in the slopes ($p>.2$). At each elbow amplitude, wrist peak velocity increased significantly with wrist amplitude ($p< 0.01$). Similar relationships were observed for wrist flexion movements. In contrast to elbow movements, both wrist movement duration and peak velocity were highly dependent on the amplitude of concurrent elbow movement.

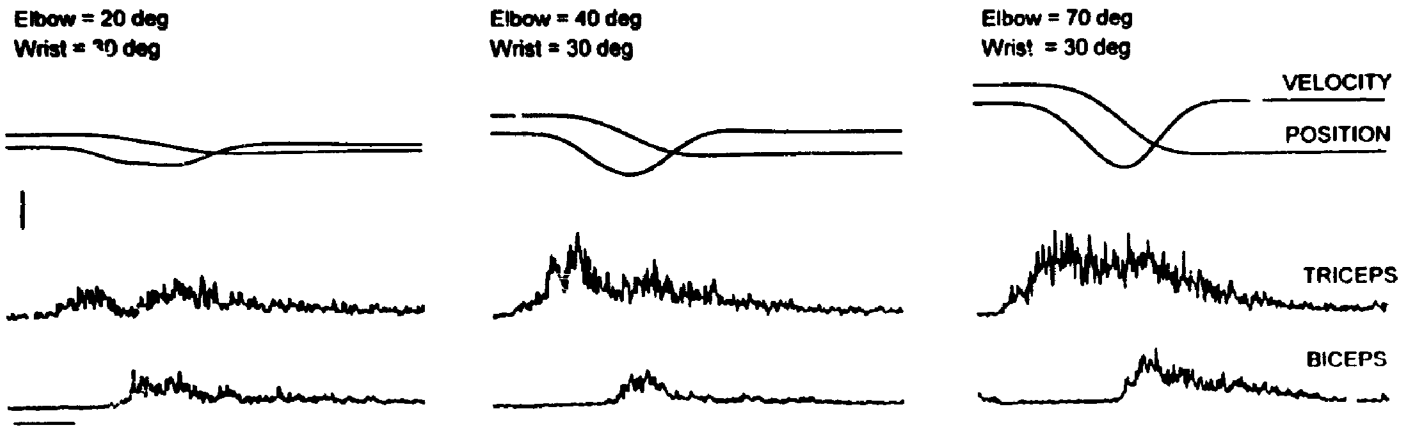
B. Muscle activation patterns

In many single joint movements both the magnitude and the duration of the initial agonist burst (AG1) increase with movement amplitude (Hallett and Marsden, 1979; Brown and Cooke, 1984). In the present two-joint task, the changes in AG1 magnitude with movement amplitude at both the elbow and wrist joints were qualitatively similar to those observed in movements about a single joint. For example, Fig. 11 shows that phasic activity in the elbow agonist generally increased as amplitude increased during extension/extension movements. Similarly, in Fig. 12 phasic activity in the wrist agonist increased as wrist amplitude increased from 20 to 40 deg during extension/extension movements.

Given that there were no significant changes in the elbow movement kinematics at any given amplitude as a function of wrist amplitude, we examined the underlying EMGs in more detail to determine the strategy used by the CNS to produce such consistent trajectories. Fig. 13 shows movement kinematics and associated EMGs for constant amplitude (40 deg) elbow flexion movements made in conjunction with three different amplitudes of wrist movement. As seen previously, there was little change in elbow kinematics as the wrist movement amplitude increased. In addition, it

Figure 11

Qualitative changes in elbow EMG activity as a function of amplitude. In each set of records are shown averaged position, velocity and EMG activity for elbow extension movements of three amplitudes (20, 40 and 70 deg) that were combined with 30 deg wrist extension movements. Traces are the average of 15 movements. Records were aligned to elbow movement start for averaging. Vertical position and velocity calibration represents 40 deg and 230 deg/sec respectively. Horizontal calibration represents 100 ms.


Elbow = 20 deg
Wrist = 30 deg
Elbow = 40 deg
Wrist = 30 deg
Elbow = 70 deg
Wrist = 30 deg
VELOCITY
POSITION
TRICEPS
BICEPS

appeared that phasic EMG activity related to elbow movement changed little across all conditions. This implies that reaction torques resulting from motion about the wrist produced little if any, effect on motion of the elbow and thus no significant compensation was required in terms of muscle activity to preserve a common trajectory.

In contrast, Fig. 14 shows that elbow movement clearly affected wrist movement. Constant amplitude wrist extension movements made in conjunction with elbow movements of three different amplitudes are shown. As described previously, wrist movement duration increased and peak velocity decreased as elbow amplitude increased. Interestingly however, these changes in movement kinematics were not accompanied by corresponding changes in the muscle activation patterns. In fact, the phasic agonist activity at the wrist remained remarkably similar as elbow amplitude increased.

C. Movement Onset

In addition to changes in wrist kinematics, differences were observed in the time of movement onset between the elbow and wrist joints. The graph on the left of Fig 15 shows the average time difference between elbow and wrist movement onsets as a function of wrist amplitude for all six subjects. Positive values indicate that elbow movement started before the wrist movement. In all conditions, elbow movement onset preceded wrist movement onset and this difference increased as elbow movement amplitude increased ($p< 0.08$). For example, for 20 deg wrist movements, the mean movement onset difference increased from 16 (+/-12) to 50 (+/- 20) ms as

Figure 12

Qualitative changes in wrist EMG activity as a function of amplitude. In each set of records are shown averaged position, velocity and EMG activity for wrist extension movements of three amplitudes (20, 30 and 40 deg) that were combined with 40 deg elbow extension movements. Traces are the average of 15 movements. Records were aligned to wrist movement start for averaging. Vertical position and calibration represents 40 deg and 320 deg/sec respectively. Horizontal calibration represents 100 ms.

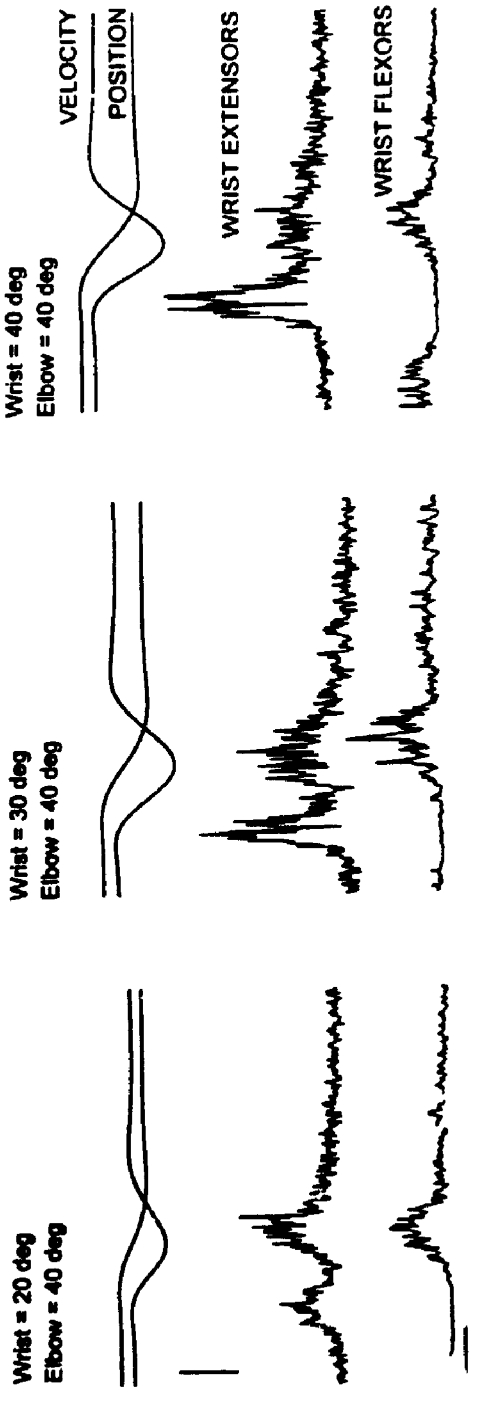
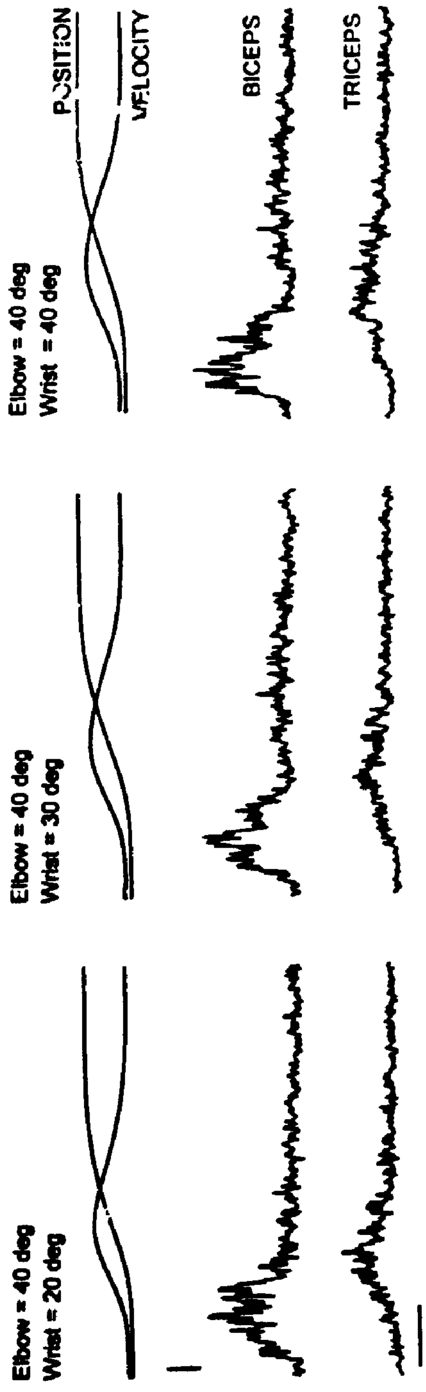

Wrist = 20 deg
Elbow = 40 deg
Wrist = 30 deg
Elbow = 40 deg
Wrist = 40 deg
Elbow = 40 deg
VELOCITY
POSITION
WRIST EXTENSORS
WRIST FLEXORS

Figure 13

Elbow EMG activity as a function of wrist amplitude. Averaged position, velocity and EMG activity for elbow flexion movements of 40 deg are shown. These movements were combined with wrist flexion movements of 20, 30 and 40 deg. Records are the average of 15 movements. Records were aligned to elbow movement start for averaging. Vertical position and velocity calibration represents 40 deg and 140 deg/sec. Horizontal calibration represents 100 ms.


Elbow = 40 deg
Wrist = 20 deg
Elbow = 40 deg
Wrist = 30 deg
Elbow = 40 deg
Wrist = 40 deg
POSITION
VELOCITY
BICEPS
TRICEPS

elbow amplitude increased from 20 deg to 70 deg.

This difference in joint movement onsets with changes in elbow amplitude was not accompanied by a similar change in the onsets of the EMG bursts occurring in elbow and wrist agonists. The right hand graph of Fig 15 shows the time difference between AG1 onsets from three subjects (in whom AG1 onsets could be clearly determined). The mean onset difference ranged from 22 (+/-15) to 30 (+/-19) ms. These values are comparable to those reported by Karst and Hasan (1991) and Wadman et al (1980) for movements about the shoulder and elbow joints. As elbow amplitude increased, the difference in AG1 onsets remained unchanged at both 30 and 40 deg wrist amplitudes ($p > 0.8$). Thus while the relative timings of movement onsets changed, this was not associated with changes in the onsets of the AG1 bursts which is normally thought to initiate movements.

D. Torque Profiles

The observation that phasic EMG activity at the wrist changed little while movement kinematics changed suggested that interactional torques arising from elbow movement may have affected the wrist trajectories. In order to determine the influence of elbow movement on wrist movement, the torques acting at the wrist joint were calculated from averaged velocity and acceleration records. Fig. 16 shows the calculated torques from the averaged data of one representative subject for a constant wrist movement amplitude of 40 deg combined with increasing elbow movement amplitudes. As elbow movement amplitude increased (from 20 to 70 deg), the peak reaction torque at the wrist increased from about 0.3 Nm to 0.8 Nm. In

Figure 14

Wrist EMG activity as a function of elbow amplitude. Averaged position, velocity and EMG activity for wrist extension movements of 40 deg are shown. These movements were combined with elbow flexion movements of 20, 40 and 70 deg. Records are the average of 15 movements. Records were aligned to wrist movement start for averaging. Vertical position and velocity calibration represents 40 deg and 220 deg/sec. Horizontal calibration represents 100 ms.

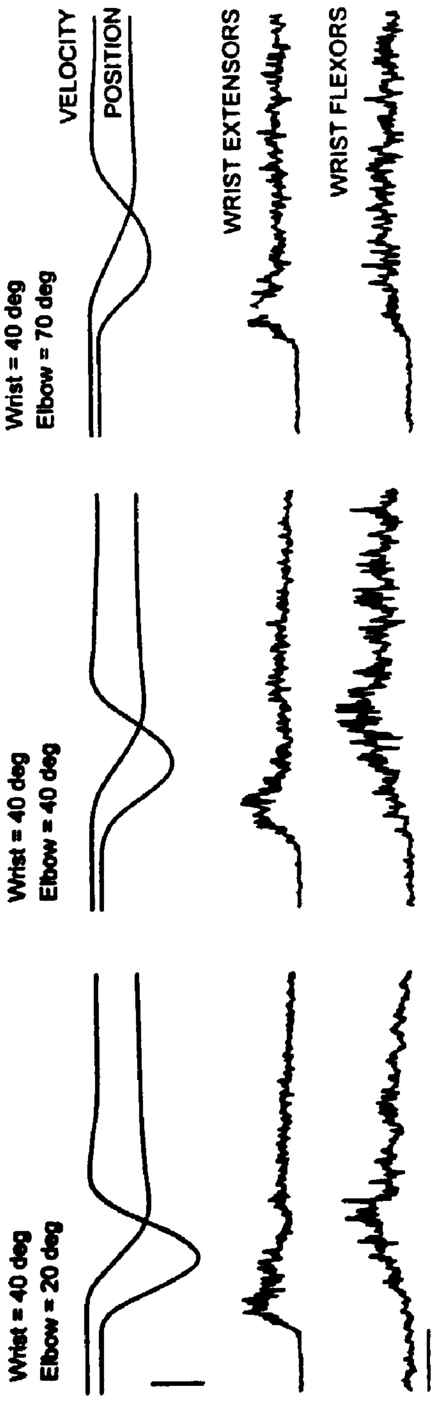
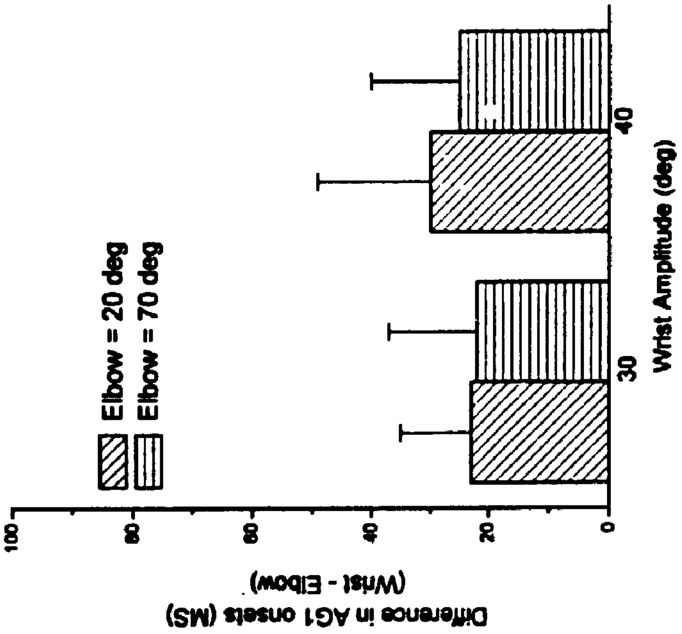
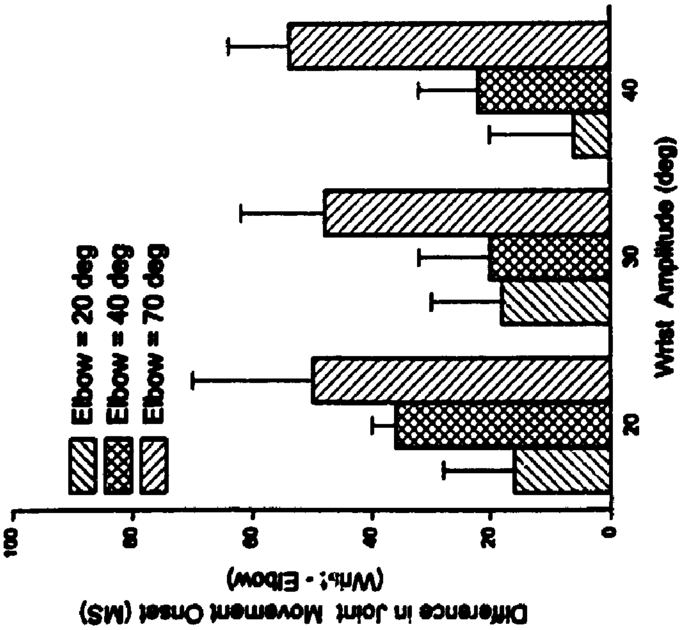

Wrist = 40 deg
Elbow = 20 deg
Wrist = 40 deg
Elbow = 40 deg
Wrist = 40 deg
Elbow = 70 deg
VELOCITY
POSITION
WRIST EXTENSORS
WRIST FLEXORS

Figure 15

Differences in movement onset and AG1 onset between the elbow and wrist joints. Average time difference between elbow flexion and wrist flexion movement onset as a function of wrist amplitude (A). Each bar represents data from 6 subjects. Average time difference between onset of phasic agonist activity at the elbow and wrist joints (B). Each bar represents data from 3 subjects. Error bars are 1 SEM.


Difference in AG1 onsets (MS)
(Wrist - Elbow)
100
80
60
40
20
0
Elbow = 20 deg
Elbow = 70 deg
30
40
Wrist Amplitude (deg)


Difference in Joint Movement Onset (MS)
(Wrist - Elbow)
100
80
60
40
20
0
Elbow = 20 deg
Elbow = 40 deg
Elbow = 70 deg
20
30
40
Wrist Amplitude (deg)

contrast, the amplitude of the peak muscle torque only increased from about 0.8 Nm to 1.0 Nm. Since the reaction torque (which opposed the movement) increased, and there was no corresponding increase in the muscle torque, the net torque driving the wrist decreased. Consequently, larger elbow movements were associated with smaller wrist accelerations. It should be noted that since the magnitude of the centripetal torque was relatively small (the range was .01 to .08 Nm) this term was not plotted in Fig. 16.

It is of particular interest to note in this figure that onset of the net wrist torque (and therefore wrist acceleration onset) gradually shifts at larger elbow amplitudes. As shown previously, changes in joint onset times did not result from a change in EMG onsets. Examination of the torques indicated that this shift was due to the interaction of elbow reaction torques and wrist muscle torques. At 20 deg elbow amplitude, the magnitude of the wrist muscle torque was larger than the magnitude of the elbow reaction torque at movement start and wrist acceleration began at about the same time as elbow acceleration. However, for the 70 deg elbow movement the magnitudes of the wrist muscle torque and elbow reaction torques were approximately equal at the start of movement. Thus, the time at which the muscle torque exceeded the elbow reaction torque was delayed and consequently the onset of wrist acceleration was delayed.

In contrast, wrist movement had little influence on elbow movement, as expected. The torques acting at the elbow joint were calculated from averaged velocity and acceleration records. Fig. 17 shows the calculated torques from the averaged data

Figure 16

Calculated torques acting at the wrist joint. Records of the reaction, muscle and net torque acting at the wrist during wrist extension movements of 40 deg are shown. These movements were combined with elbow extension movements of 20, 40 and 70 deg. Traces are the average of 15 movements. Records were aligned to elbow movement start for averaging.

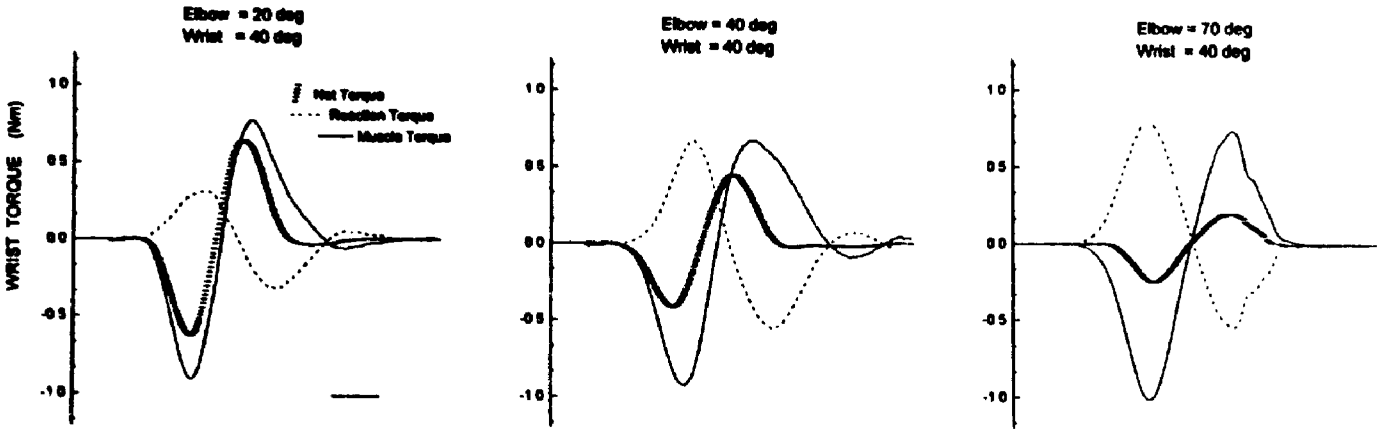
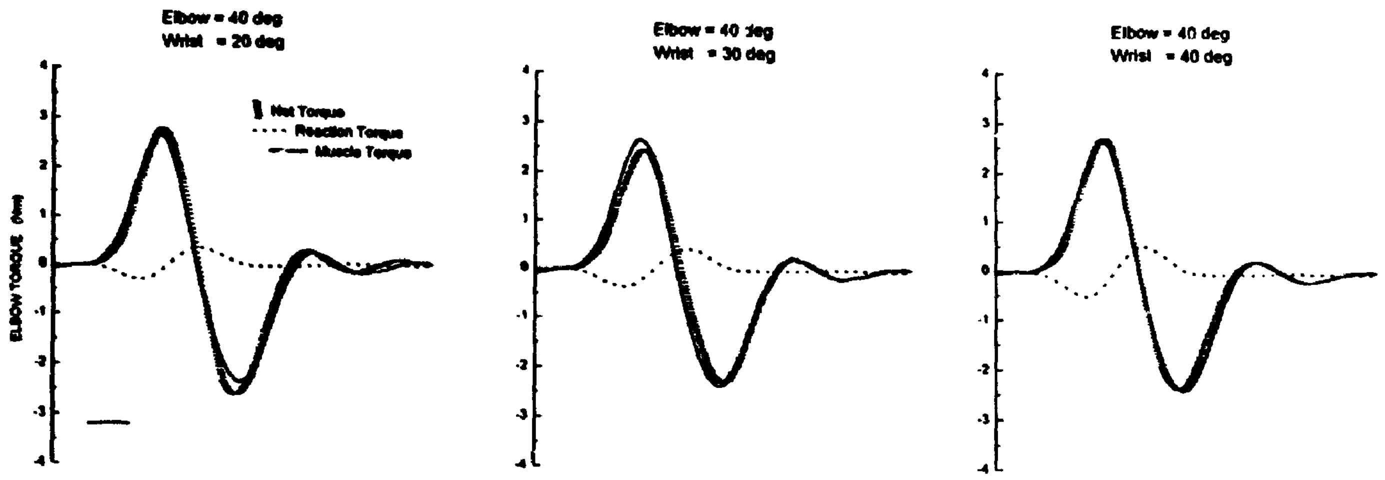

Elbow = 20 deg
Wrist = 40 deg
Net Torque
Reaction Torque
Muscle Torque
WRIST TORQUE (Nm)
1.0
0.5
0.0
-0.5
-1.0
Elbow = 40 deg
Wrist = 40 deg
1.0
0.5
0.0
-0.5
-1.0
Elbow = 70 deg
Wrist = 40 deg
1.0
0.5
0.0
-0.5
-1.0

Figure 17

Calculated torques acting at the elbow joint. Records of the reaction, muscle and net torque acting at the elbow during elbow flexion movements of 40 deg are shown. These movements were combined with wrist flexion movements of 20, 30 and 40 deg. Traces are the average of 15 movements. Records were aligned to elbow movement start for averaging.


Elbow = 40 deg
Wrist = 20 deg
Net Torque
Reaction Torque
Muscle Torque
ELBOW TORQUE (Nm)
4
3
2
1
0
-1
-2
-3
-4
Elbow = 40 deg
Wrist = 30 deg
Elbow = 40 deg
Wrist = 40 deg

from the same subject for constant elbow movement amplitude of 40 deg combined with increasing wrist movement amplitudes. As can be seen clearly, as wrist movement amplitude increased (from 20 to 40 deg) there is little change in both the muscle and net torque acting at the elbow.

3.4 Summary

The results of this study have shown that in moving from single joint horizontal planar movements to two-joint horizontal planar movements, the known relations between phasic muscle activity and kinematic variables at the distal joint have been significantly altered. In contrast to the previous study where the same velocity profile was associated with different patterns of muscle activity, in this study, a common pattern of muscle activity was associated with different velocity profiles. Analysis of the torques acting at the wrist joint demonstrated that the modifications in the velocity profiles resulted in part, from the influence of the torques resulting from elbow acceleration.

REPROGRAMMING OF MUSCLE ACTIVATION PATTERNS AT THE WRIST DURING PLANAR TWO-JOINT ARM MOVEMENTS IN OPPOSITE DIRECTIONS

4.1 Introduction

The results from Chapter 3 showed that during two-joint movements (in which the two joints rotated in the same direction), the wrist movement trajectory was significantly influenced by reaction torques resulting from elbow movement. Furthermore, a basic pattern consisting of alternating bursts in the agonist and antagonist was observed at the wrist joint despite changes in target location, and elbow joint amplitude. In contrast, no significant changes were observed in the elbow kinematics or muscle activation patterns. In order to further evaluate the effects of elbow reaction torque directionality on wrist movement, two-joint movements in which the wrist and elbow rotated in opposite directions (i.e. flexion/extension and extension/flexion) were studied. In this configuration the reaction torques resulting from elbow movement act in the same direction as the intended wrist movement and would therefore, assist wrist movement. Since increases in elbow acceleration result in larger reaction torques, the question that arises is how are the muscle activation patterns at the wrist joint modified in order to account for such increases.

4.2 Methods

A. Experimental Paradigm

Five normal subjects (aged 24-55) with no known history of motor system disorders participated in this study. Subjects performed flexion and extension movements about the elbow and wrist joints in a step-tracking paradigm. A stick figure target composed of two connected bars, representing the forearm and hand, was displayed on a television monitor. The configuration of the two connected bars could be altered to independently set individual elbow and wrist angles. The subject's actual forearm and hand positions were displayed as two connected lines on the same monitor (see top insert in Fig. 18). The target stick figure switched at a regular rate (every 5 seconds) between the initial and final elbow and wrist positions. The display of the subject's forearm and hand position was refreshed every 10 msec. Subjects were required to superimpose their forearm and hand positions on the target stick figure by moving the lines into the bar. The width of each bar corresponded to a movement amplitude of approximately 3 degrees. Subjects were instructed to move "fast and accurately" between the target bars. Movements that were off the target amplitude by greater than 5 degrees were discarded. This resulted in approximately 5% of the movements being discarded.

Subjects were seated comfortably and grasped a vertical rod attached to a biarticulated manipulandum which rotated in the horizontal plane about vertical axes at the elbow and wrist joints. Each subject's shoulder was adducted to 90 deg, with the forearm semi-prone. The forearm and hand were supported along the length of the forearm and hand segments of the manipulandum. The initial position for initiating movements was 35 degrees of elbow extension (0 deg equalling full extension) for the forearm and 10 deg of wrist flexion for the hand. From this position subjects made elbow flexion/wrist extension movements of various amplitudes, and returned to the initial position by making elbow extension/wrist flexion movements. Subjects performed all movements with their dominant arm.

Subjects were asked to make a combined elbow flexion/wrist extension movement followed by an elbow extension/wrist flexion movement. This sequence was then repeated. Three target wrist amplitudes of 10, 30 and 50 deg were combined with three target elbow amplitudes of 10, 40 and 70 deg. This resulted in a total of 9 separate combinations of two-joint movement targets which were presented in a random order, in a single session. In each movement condition, a block of 30 movements was performed consisting of 15 elbow flexion/wrist extension movements and 15 elbow extension/wrist flexion movements. Presentation of each new block was preceded by a rest period of 2-3 minutes. Due to the novelty of the task condition, subjects made approximately 100 practice movements at the start of the experiment to learn the required movement.

B. Data Recording

The angular positions of the two joints were obtained from potentiometers. Surface EMGs were recorded from biceps, lateral head of triceps, flexor carpi radialis and extensor carpi radialis with bipolar electrodes separated by 1 cm. All data were digitized online (12 bit) at 500 Hz. EMGs were filtered (10 to 1000 Hz) and subsequently full wave rectified. The data were then stored for later off-line analysis.

C. Data Analysis

The times of the start and end of movement were determined from individual movements by digital differentiation of the position signal using a threshold of 8 deg/sec. These times were then used in determining movement duration. Mean values for movement start and movement duration from each subject were used to calculate means and standard errors across all subjects. The moment of inertia of each subject's forearm and hand segments were calculated from Dempster's estimates reported in Winter (1991). The muscle torques acting at the elbow and wrist were calculated using the equations of motion described by Hollerbach and Flash (1982) and Karst and Hasan (1991). (For further details see previous chapter)

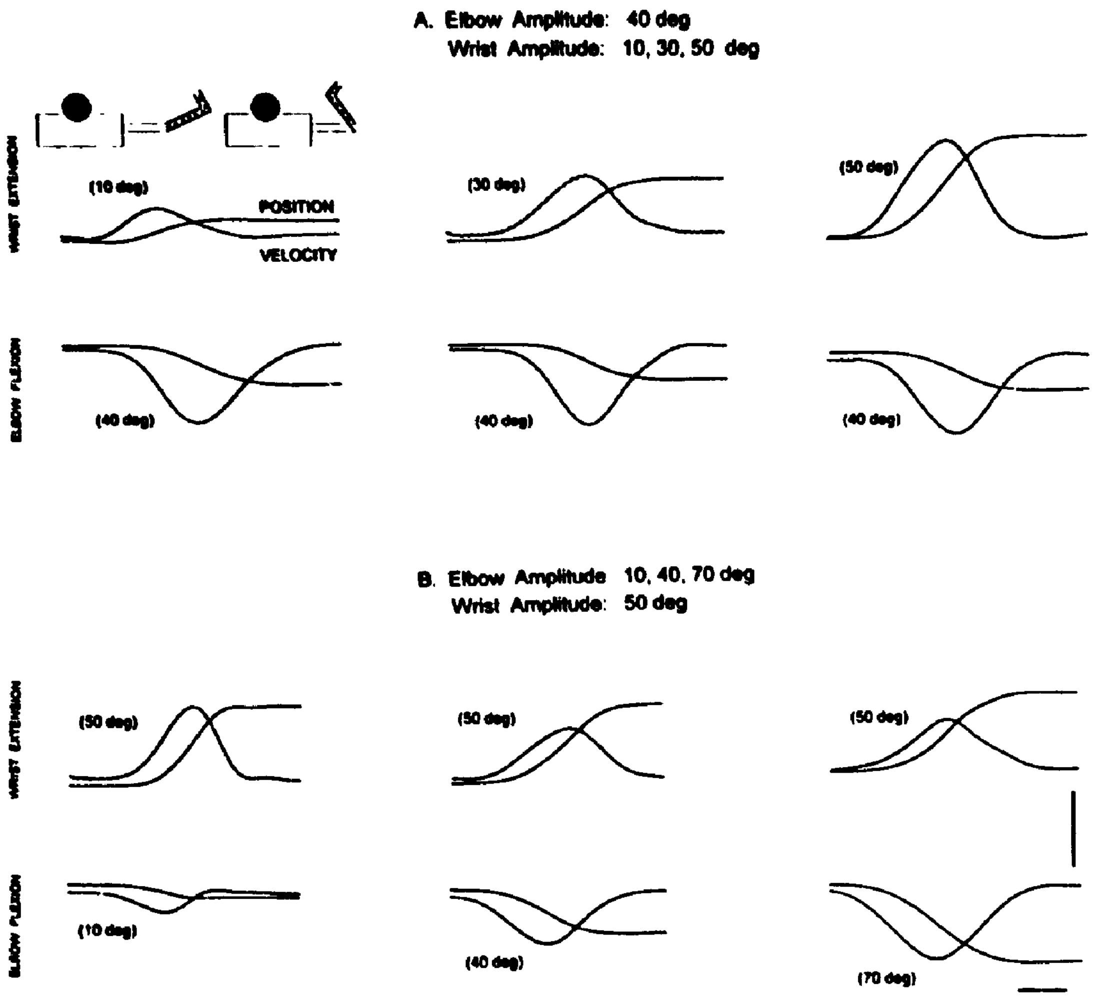
4.3 Results

A. Movement Kinematics

Representative data from some of the different two-joint movement conditions used in this experiment are illustrated in Fig. 18. Averaged position and velocity records of elbow and wrist movements from one representative subject are shown. In all conditions the wrist and elbow rotated in opposite directions, that is, flexion/extension or extension/flexion. In Fig. 18A, wrist extension movements of three different amplitudes (10, 30 and 50 deg) combined with elbow flexion of 40 deg are shown. Note that wrist movement duration and peak velocity increased as wrist amplitude increased. There was very little qualitative change in the shape of the

Figure 18

Two-joint elbow and wrist movements in opposite directions. Records of position and velocity from combined elbow flexion/wrist extension movements are shown. In (A) wrist extension movements of three amplitudes (10,30 and 50 deg) were combined with 40 deg elbow flexion movements. In (B) elbow flexion movements of three amplitudes (10,40 and 70 deg) were combined with 50 deg wrist extension movements. Traces are the average of 15 movements. Records were aligned to movement start for averaging. Vertical velocity calibration represents 200 deg/sec (A) and 400 deg/sec (B) respectively. Horizontal calibration represents 100 ms.

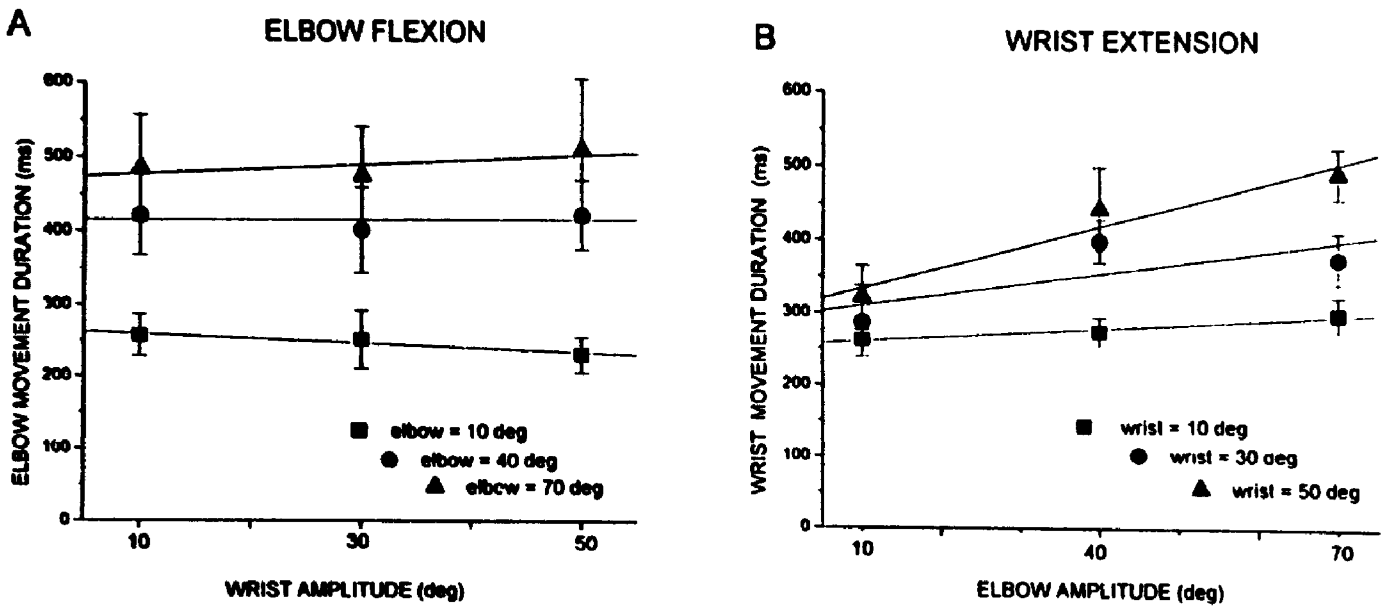

A. Elbow Amplitude: 40 deg
Wrist Amplitude: 10, 30, 50 deg
WRIST EXTENSION
ELBOW FLEXION
(10 deg)
POSITION
VELOCITY
(30 deg)
(50 deg)
(40 deg)
(40 deg)
(40 deg)
B. Elbow Amplitude 10, 40, 70 deg
Wrist Amplitude: 50 deg
WRIST EXTENSION
ELBOW FLEXION
(50 deg)
(50 deg)
(50 deg)
(10 deg)
(40 deg)
(70 deg)

velocity profile of the elbow as wrist movement amplitude increased. Fig. 18B illustrates wrist extension movements of 50 deg combined with elbow flexion movements of three different amplitudes (10, 40 and 70 deg) from the same subject. As expected, elbow movement duration and peak velocity increased with elbow amplitude. In contrast to the consistent elbow profiles observed in Fig. 18A, there were quite striking changes in the shape of the wrist velocity profile as elbow amplitude increased. In general, wrist movement duration increased and peak velocity decreased.

Quantitatively, wrist kinematics were also affected to a greater extent by concurrent elbow movements than were elbow kinematics by wrist movements. Fig. 19 shows the changes in movement duration at one joint plotted as a function of movement amplitude of the other joint. In Fig. 19A, elbow movement duration is plotted as a function of wrist amplitude. There was little change in elbow movement duration with wrist amplitude as indicated by the slopes of the best fit linear regression lines (slopes ranged from -0.7 to 0.7 ms/deg). Note that at any given wrist amplitude, elbow movement duration increased as elbow amplitude increased. Fig. 19B shows the changes in wrist movement duration as a function of elbow amplitude. In contrast to elbow movements, wrist movement duration tended to increase as elbow amplitude increased (slopes of the linear regression lines ranged from 0.6 to 3 ms/deg). Similar relationships were observed for the combination of elbow extension/wrist flexion movements. Wrist movement duration, particularly at the larger amplitudes, appeared to be more affected by the amplitude of concurrent

Figure 19

Movement duration-amplitude relations. Elbow flexion movement duration is plotted as a function of wrist amplitude (A) and wrist extension movement duration is plotted as a function of elbow amplitude (B). Each point is the average obtained from 5 subjects. Error bars are 1 SEM. Solid lines are the best-fit linear regression lines.


A
ELBOW FLEXION
ELBOW MOVEMENT DURATION (ms)
0
100
200
300
400
500
600
10
30
50
WRIST AMPLITUDE (deg)
elbow = 10 deg
elbow = 40 deg
elbcw = 70 deg
B
WRIST EXTENSION
WRIST MOVEMENT DURATION (ms)
0
100
200
300
400
500
600
10
40
70
ELBOW AMPLITUDE (deg)
wrist = 10 deg
wrist = 30 deg
wrist = 50 deg

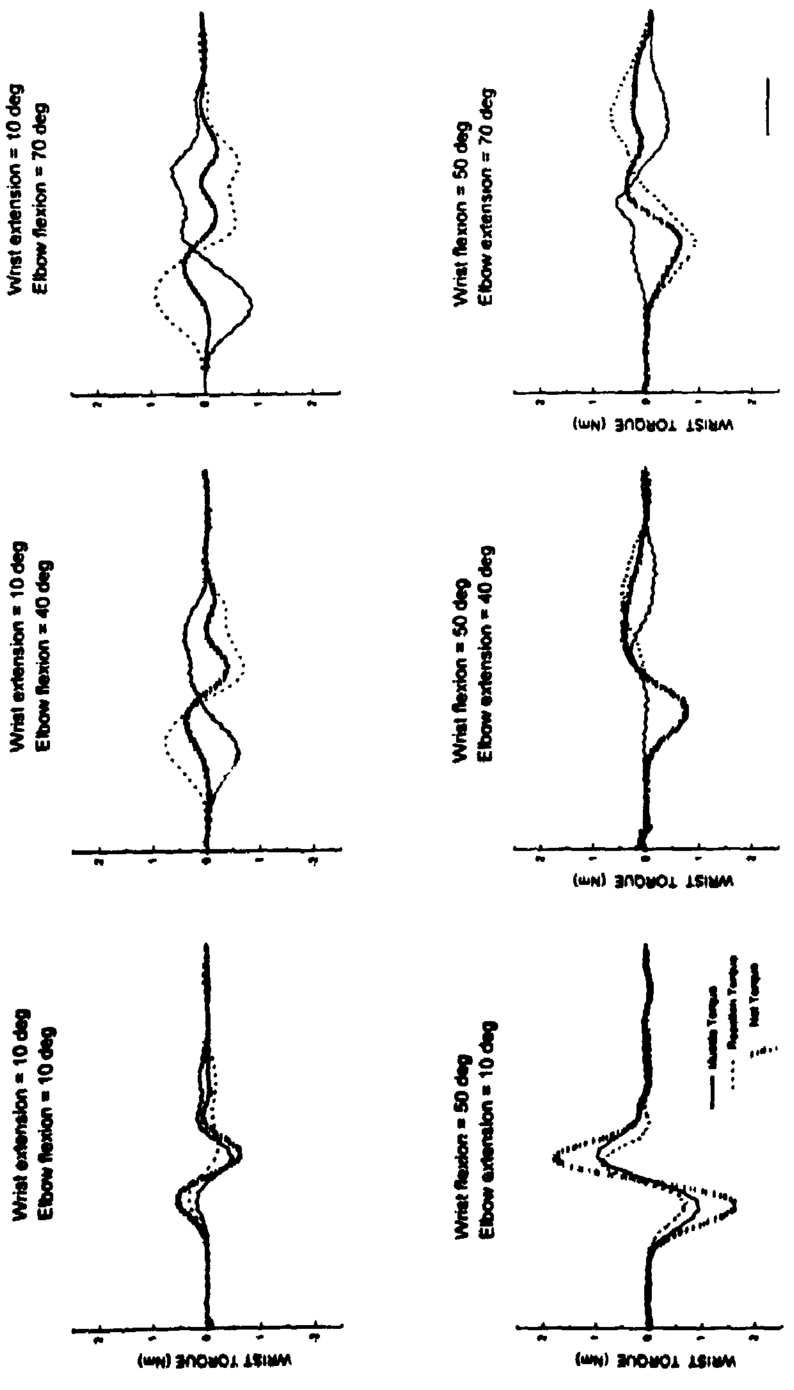
elbow movement than was elbow movement duration by the amplitude of the wrist movement.

B. Torque Profiles

In the previous experiment it was shown that during two joint wrist and elbow movements in the same direction, changes in wrist kinematics were directly related to joint interactional effects. The changes in wrist kinematics as a function of elbow movement amplitude in the present experiment, suggested that interactional torques arising from elbow movement were in some manner, influencing the wrist trajectory. In order to determine the nature of this influence, the torques acting on the wrist joint were calculated from averaged velocity and acceleration records. Fig. 20 shows the calculated wrist torques from the averaged data of one representative subject. Torques are shown for wrist extensions of 10 deg combined with increasing elbow flexion amplitudes (upper panel) and of wrist flexions of 50 deg combined with increasing elbow extension amplitudes (lower panel). In all conditions, the reaction torque at the wrist resulting from elbow movement acted in the same direction as the net wrist torque. Thus, movement about the elbow produced a torque that assisted the intended wrist movement. As elbow amplitude increased (from 10 to 70 deg) and the magnitude of elbow acceleration increased, the peak reaction torque at the wrist increased and indeed, exceeded the net torque at the wrist. This is particularly evident in large elbow movements combined with small wrist movements (upper panel). Under such conditions the wrist muscle torque reversed direction and *opposed* the intended movement. Consequently, the net torque driving the wrist

Figure 20

Calculated torques acting at the wrist joint. Records of the reaction, muscle and net torques acting at the wrist during wrist flexion movements of 50 deg are shown. These movements were combined with elbow extension movements of 10, 40 and 70 deg. Traces are the average of 15 movements.


Wrist extension = 10 deg
Elbow flexion = 10 deg
Wrist extension = 10 deg
Elbow flexion = 40 deg
Wrist extension = 10 deg
Elbow flexion = 70 deg
Wrist flexion = 50 deg
Elbow extension = 10 deg
Wrist flexion = 50 deg
Elbow extension = 40 deg
Wrist flexion = 50 deg
Elbow extension = 70 deg
WRIST TORQUE (Nm)
WRIST TORQUE (Nm)
WRIST TORQUE (Nm)
WRIST TORQUE (Nm)
2
1
0
-1
-2
Muscle Torque
Reaction Torque
Net Torque

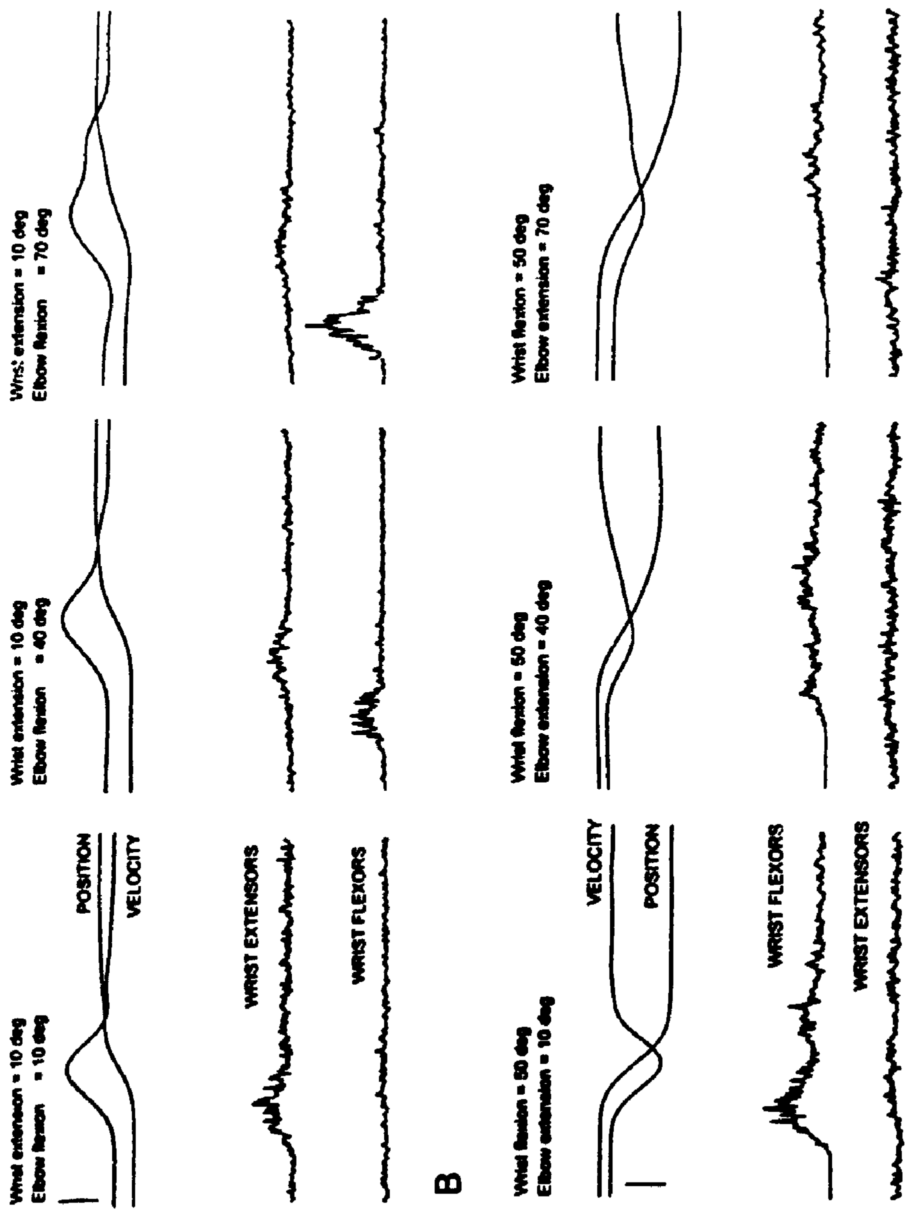
movement decreased and larger elbow movements were associated with smaller wrist accelerations. In contrast, the magnitudes of the peak elbow reaction torque and the net wrist torque were approximately equal in conditions where large amplitude elbow movements were combined with large amplitude wrist movements (lower panel). Thus, as elbow amplitude increased, the desired movement was produced by decreasing the magnitude of the wrist muscle torque rather than reversing its direction.

C. Muscle Activation Patterns

The changes in the calculated wrist muscle torque suggested that the muscle activation patterns at the wrist were being modified in relation to elbow acceleration. In Fig. 21 typical EMG activity from wrist extension movements of 10 deg (A) and wrist flexion movements of 50 deg (B) made in conjunction with elbow movements of three different amplitudes are shown. As described previously, wrist movement duration increased as elbow amplitude increased. In addition, note that the wrist movement profile lost its smooth, bell-shaped profile as elbow amplitude increased. This was particularly noticeable when wrist movements were combined with large amplitude (70 deg) elbow movements (right hand records). When small amplitude wrist movements were combined with small amplitude elbow movements, phasic activity in the agonist started prior to movement start (Fig 21A - left hand record). As the elbow amplitude increased, phasic activity in the *antagonist* occurred prior to movement start and was followed by phasic activity in the agonist. In addition, there was a qualitative increase in the magnitude of phasic antagonist activity with an

Figure 21

Wrist EMG activity as a function of elbow amplitude. In each set of records are shown averaged position, velocity and EMG activity for wrist extension movements. In (A) wrist extension movements of 10 deg were combined with elbow flexion movements of 10, 40 and 70 deg. In (B) wrist extension movements of 50 deg were combined with elbow flexion movements of 10, 40 and 70 deg. Records are the average of 15 movements. Records were aligned to wrist movement start for averaging. Vertical velocity calibration represents 200 deg/sec. Horizontal calibration represents 100 ms.


A
Wrist extension = 10 deg
Elbow flexion = 10 deg
POSITION
VELOCITY
WRIST EXTENSORS
WRIST FLEXORS
Wrist extension = 10 deg
Elbow flexion = 40 deg
Wrist extension = 10 deg
Elbow flexion = 70 deg
B
Wrist flexion = 50 deg
Elbow extension = 10 deg
VELOCITY
POSITION
WRIST FLEXORS
WRIST EXTENSORS
Wrist flexion = 50 deg
Elbow extension = 40 deg
Wrist flexion = 50 deg
Elbow extension = 70 deg

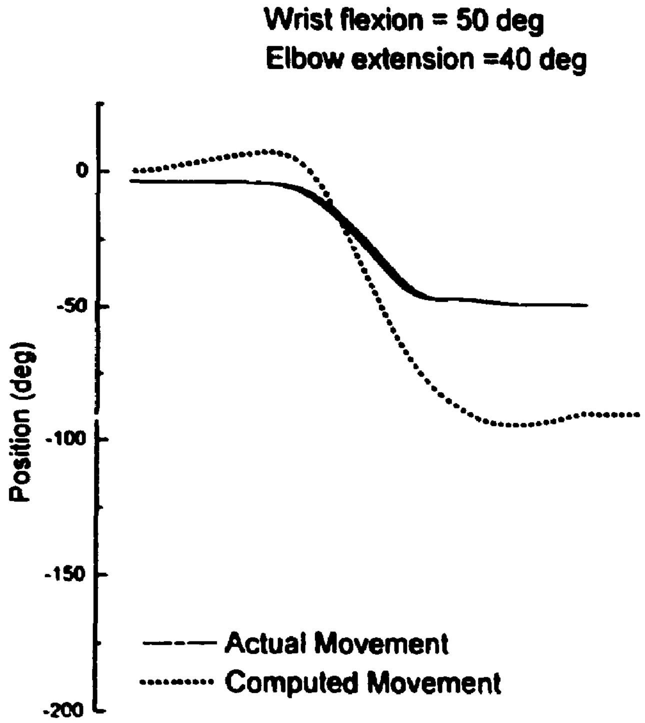
associated qualitative decrease in agonist activity as elbow amplitude increased. When large amplitude wrist movements were combined with small amplitude elbow movements (Fig 21B - left hand records) phasic activation of the agonist was seen at the start of movement, similar to that observed in small amplitude wrist movements. As elbow amplitude increased, the magnitude of phasic agonist activity decreased significantly. In these movements there was no corresponding increase in antagonist activity. Thus the calculated changes in wrist muscle torque corresponded directly to the observed changes in the pattern of muscle activation at the wrist joint.

D. Theoretical effect of maintaining the same wrist muscle torque

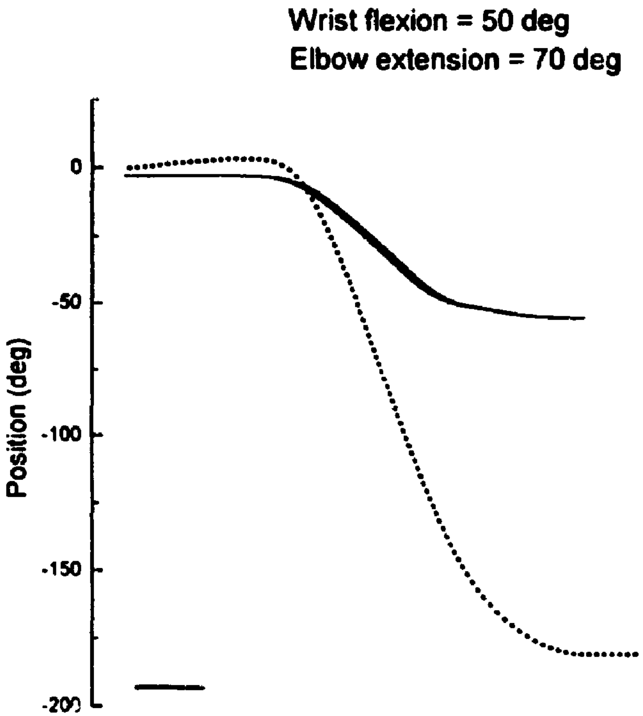
In order to assess the function of the changes in the EMG activation and resulting muscle torques, wrist movement was computed under the condition that the wrist muscle torque did not change as elbow amplitude increased. Wrist acceleration was computed for movements made with elbow amplitudes of 40 and 70 deg respectively. This acceleration was calculated from the actual reaction torques produced by elbow acceleration in each condition (under the assumption that wrist position was 50 deg), as well as the wrist muscle torque produced during 50 deg wrist movements combined with 10 deg elbow movements. Wrist position was then computed by double integration of the acceleration curve. Fig. 22 shows the actual and computed movements for wrist flexion movements of 50 degrees combined with elbow movements of 40 and 70 degrees. It is striking to note that by maintaining the same muscle torque, the wrist movement would have increased from 50 degrees to approximately 100 and 170 deg respectively. Clearly, compensation by decreasing

Figure 22

Comparison of actual and computed wrist position. Records of wrist movement amplitude computed under the condition that wrist muscle torque did not change for wrist movements of 50 deg combined with elbow extension movements of 40 and 70 deg. Horizontal calibration represents 100 ms.



Wrist flexion = 50 deg
Elbow extension =40 deg



Wrist flexion = 50 deg
Elbow extension = 70 deg

agonist activity or by increasing antagonist activity was necessary to ensure that the correct movement amplitude would be achieved.

4.4 Summary

The paradigm used in this study was an extension of the study described in Chapter 3 designed to evaluate the effects of elbow reaction torque directionality on wrist movement during a two-joint movement task. The results from the previous study demonstrated that when the two joints moved in the same direction, a basic pattern consisting of alternating bursts in the agonist and antagonist was observed at the wrist joint. This pattern was preserved despite changes in joint amplitude and target location. The interesting finding of the present study was that when the same two joints moved in opposite directions, distinct patterns of muscle activation were observed at the wrist joint that were directly dependent on the magnitude of the reaction torques resulting from elbow acceleration.

In conditions where the magnitude of the elbow reaction torque was quite small, the wrist agonist was activated first. As the magnitude of the elbow reaction torque increased two different strategies were used to account for the these changes. If the elbow reaction torque greatly exceeded the net wrist torque, the wrist antagonist was activated first to oppose the reaction torque resulting from elbow acceleration. In such conditions, phasic activity in the wrist agonist followed the activity in the antagonist in order to counter the later reaction torque which acted in a direction to decelerate the movement. If the elbow reaction torque was approximately equal to the net wrist torque, the wrist agonist activity was decreased such that wrist movement would be driven by elbow reaction torques. The implication of these findings will be addressed in the Discussion.

INFLUENCE OF VISUAL FEEDBACK INFORMATION ON INTER-JOINT COORDINATION

5.1 Introduction

The generation of a visually guided goal-directed movement requires the transformation from a visual representation of the target into the appropriate motor commands (Soechting and Flanders, 1989). The role of visual information in movement control has been studied extensively since Woodworth (1899) first described the influence of visual feedback on the accuracy of motor performance. Since then a major focus of visuo-motor research has concentrated on establishing the role of visual feedback in regulating both movement accuracy and kinematics (see Jeannerod, 1988 for review).

Recently, it has been suggested that visual information can have a much more significant role in controlling specific parameters of the movement (Cordo and Flanders, 1989), as well as in coordinating movement of limb segments during multi-joint movements (Sainburg and Ghez, 1994). To date, however, little is known about the nature of the external visual target/environment that may influence movement coordination. Many studies have tended to emphasize the influence of visual or kinaesthetic information on movement accuracy through analysis of specific movement errors (Blouin et al, 1993; Darling and Miller, 1993; Tillery et al, 1991; Gentilucii and Negrotti, 1994;). There have been few attempts to discern the role of visual information on movement programming during multi-joint movements.

Sainburg et al (1993) studied multi-joint slicing movements in two deafferented subjects. The wrist paths during these movements were found to be quite variable, curved and nonplanar. Furthermore, motions of the shoulder and elbow joints were temporally decoupled. Interestingly, when the patients were able to view their limb during the movement, their wrist paths became more linear and planar, although the timing relationships between the joints did not change. The authors proposed that improvements in motor performance with vision, indicates that the primary role of vision is to update an internal model of limb biomechanical properties used to program movement.

Given this hypothesis, does the CNS specifically require input about limb dynamics by viewing the physical structure of the limb, or can this information be extracted from a visual representation of arm movement? Ghez et al (1995) have shown that both handpath information provided by information from a cursor on a computer screen, and vision of the limb, are equally useful in improving movement accuracy in deafferented patients. The authors propose that both types of visual feedback information provide important information about the dynamic properties of the limb for movement planning. It would appear from this study that the CNS does not specifically require input about limb dynamics by viewing the physical structure of the limb. The question of interest is what is the minimum level of abstraction (of arm representation) required for visuo-motor processing and how is inter-joint coordination influenced by the nature of the visual feedback representation.

The purpose of this study was to specifically determine whether the characteristics of visual feedback information influence coordination during a two-joint planar movement involving the wrist and elbow joints. This was particularly important in light of the fact that an "unusual" movement representation system (i.e. the stick figure display) had been utilized in the previous experiments (Chapters 3 and 4). Thus, a novel paradigm was developed in which *both* the limb position as well as the endpoint targets could be presented as progressively abstract visual representations on a computer monitor. The paradigm was specifically designed in this manner to maintain congruence between the target and limb position representations so as not to introduce another level of complexity. An additional condition was included in which subjects were required to point to physical targets. The kinematic relationship between the joints as well as the underlying muscle activation patterns under each of the visual feedback conditions were analyzed.

5.2 Methods

A. Experimental Paradigm

Six normal subjects (aged 25-34) with no known history of motor system disorders participated in this study. Subjects performed two-joint flexion and extension movements about the elbow and wrist joints in a step-tracking paradigm under three separate visual feedback conditions. In addition, all subjects performed a pointing task to physical targets on a pegboard. During all the tasks subjects were seated comfortably and grasped a vertical rod attached to a biarticulated manipulandum which rotated in the horizontal plane about vertical axes at the elbow and wrist joints. Each subject's shoulder was abducted to 90 deg, with the forearm semi-prone. The forearm and the hand were supported along the length of the forearm and hand segments of the manipulandum. Subjects made flexion movements first followed by extension movements. The initial position for initiating movements was 50 degrees of elbow extension (0 deg equalling full extension) for the forearm and 10 degrees of wrist extension for the hand. From this position subjects made elbow flexion/wrist flexion movements of various amplitudes, and returned to the initial positior by making elbow extension/wrist extension movements. Subjects performed all movements with their dominant arm.

It should be noted that the position of manipulandum allowed subject's to have peripheral vision of their arm during the movements. In order to determine whether this peripheral vision influenced movement coordination, the complete experimental protocol was repeated in one additional subject in which vision of the arm was blocked by placing a cardboard box over the manipulandum. This box was removed during movements made under the physical target condition.

Target Conditions

During the step-tracking task subjects were seated comfortably in front of a television monitor. Subjects were asked to perform two-joint movements under the three conditions described below (see Fig. 23). It should be noted that the same movements were required in all four target conditions.

(i) Segment Angle Display

A stick figure target composed of two connected bars, representing the forearm and hand was displayed on a television monitor. The configuration of the two connected bars could be altered to independently set individual elbow and wrist angles. The subject's actual forearm and hand positions were also displayed as two connected lines on the same monitor. The target stick figure switched at a regular rate (every 5 seconds) between the initial and final elbow and wrist positions. The subject's position was refreshed every 10 msec. Subjects were required to superimpose their forearm and hand positions on the target figure by moving the lines into the bar in response to a tone. The width of each bar corresponded to a movement amplitude of approximately 3 degrees.

(ii) End Points with Feedback Display

Two circular targets presented on the computer monitor indicated the initial and final position of the desired movement in hand space. The subject's hand position was displayed as a smaller circle. Both target circles were continuously displayed and subject's were required to move their elbow and wrist to superimpose the circle representing their actual hand position on the larger desired target circle. The subject's movement trajectory in hand space, as he/she moved between the two target positions was also displayed on the television monitor.

(iii) End Points with no Feedback Display

This condition was the same as described in (ii) with the exception that the subject's movement trajectory was not displayed on the television monitor.

(iv) Physical Targets

In this condition the television monitor was turned off and a pegboard was placed on a table underneath the manipulandum. Four target flexible stops were placed in the pegboard to define the initial and final positions of both the elbow and wrist joints. Subject's were required to move between the targets in response to a tone. A distinguishing marker was placed on all the flexible stops to ensure that the subject's had a specific location to aim for during the movement. In this condition subjects did not have any feedback of their movement trajectory.

Movement conditions

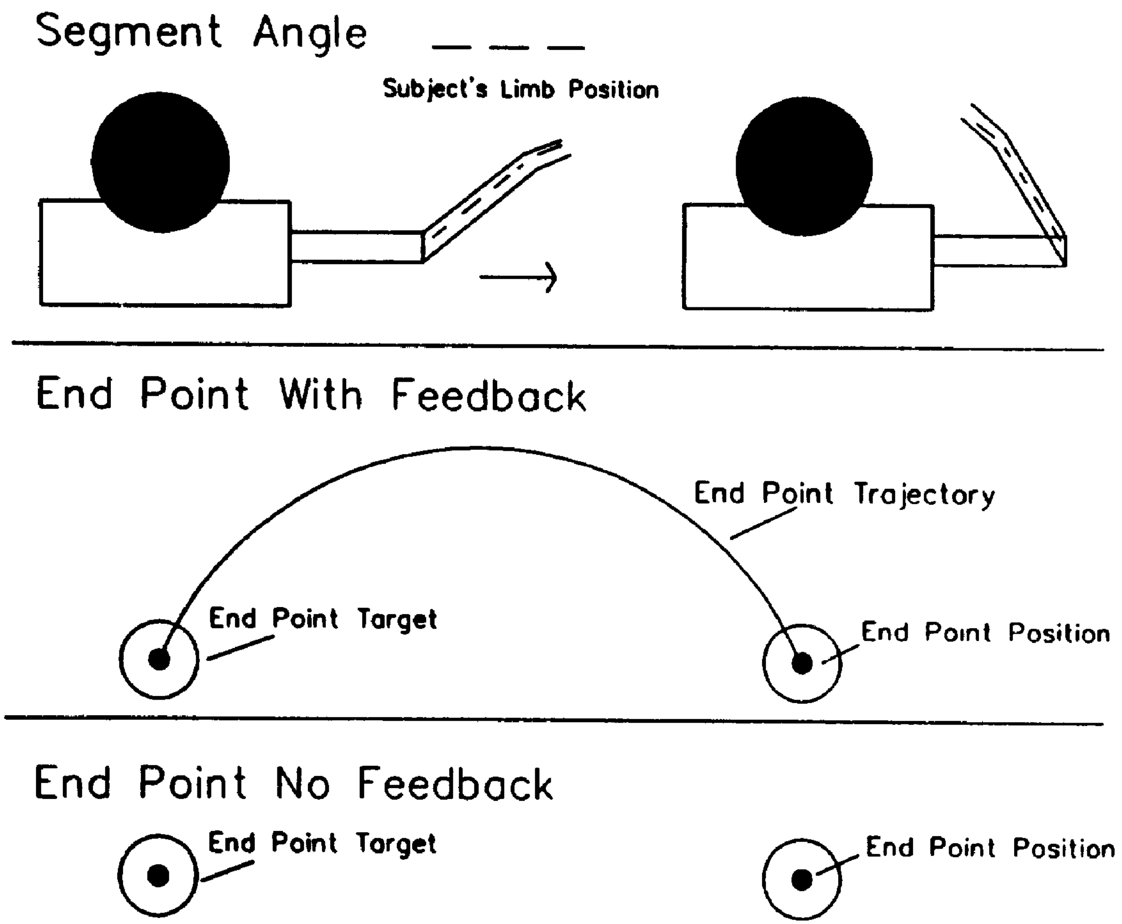
One target wrist amplitude of 40 deg was combined with two target elbow amplitudes of 20 and 70 deg. These two different elbow and wrist combinations were performed under each of the four target conditions, resulting in a total of 8 conditions. In each condition a block of 30 movements was performed consisting of 15 flexion and 15 extension movements. Presentation of each new block was preceded by a rest period of 1-2 minutes. It is important to note that movement conditions were presented in a randomized sequence for all subjects. Approximately 20-30 practice movements were made at each condition prior to data collection.

B. Data Recording

The angular positions of the two joints were obtained from precision potentiometers. Surface EMGs were recorded from biceps, lateral head of triceps, flexor carpi radialis and extensor carpi radialis with bipolar electrodes separated by

Figure 23

Visual feedback displays. The three different visual feedback displays used in this paradigm are shown. These include the segment angle, endpoint with feedback and endpoint with no feedback displays.


Segment Angle
Subject's Limb Position
End Point With Feedback
End Point Trajectory
End Point Target
End Point Position
End Point No Feedback
End Point Target
End Point Position

1 cm. All data were digitized online (12 bit) at 500 Hz. EMGs were filtered (10 to 1000 Hz) and subsequently full wave rectified. The data were then stored for later off-line analysis.

C. Data Analysis

Velocity and acceleration were obtained from individual flexion and extension movements by digital differentiation of the position signal. The times of the start and end of acceleration and deceleration were determined using a threshold of 67 deg/s^2. These times were used in determining movement start, movement duration and peak velocity. Mean values for peak velocity and movement duration from each subject were used to calculate means and standard errors across all subjects.

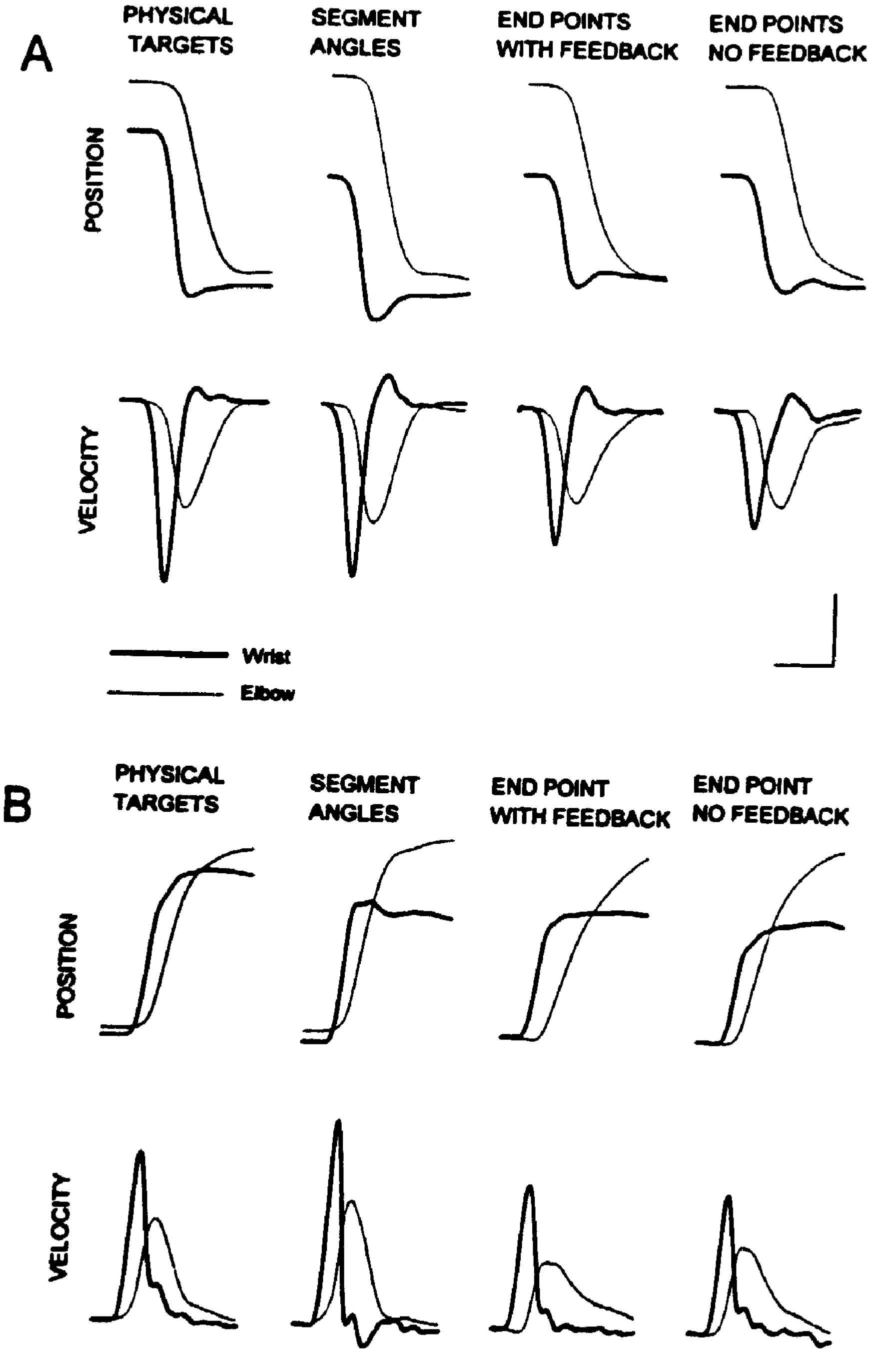
5.3 Results

A. Movement Kinematics

Representative data from the four different conditions used in this experiment are illustrated in Fig. 24. Averaged position and velocity records of elbow and wrist movements from one representative subject are shown. Fig. 24A shows elbow flexion movements of 70 deg combined with wrist flexion movements of 40 deg for movements to physical targets as well as the three visual feedback display conditions. Elbow extension movements of 70 deg combined with wrist extension movements of 40 deg are shown in Fig. 24B. All subjects performed both flexion and extension movements under all conditions. A qualitative examination of this figure shows that wrist flexion and extension movements did not terminate smoothly but had a small

Figure 24

Two-joint elbow and wrist movements made under four target conditions. Records of position and velocity from combined flexion/flexion elbow and wrist movements (A) and combined extension/extension elbow and wrist movements (B) are shown for movements to physical targets and the three visual feedback display conditions. Records were aligned to movement start for averaging. Vertical calibration represents 200 deg/sec. Horizontal calibration represents 400 ms.


A
PHYSICAL TARGETS
SEGMENT ANGLES
END POINTS WITH FEEDBACK
END POINTS NO FEEDBACK
POSITION
VELOCITY
Wrist
Elbow
B
PHYSICAL TARGETS
SEGMENT ANGLES
END POINT WITH FEEDBACK
END POINT NO FEEDBACK
POSITION
VELOCITY

period of oscillation at the end of movement. Although the elbow velocity profile was generally bell shaped, it tended to be more asymmetric in both of the endpoint (hand space) display conditions. These findings were consistent across all subjects.

In Fig. 25 changes in kinematic parameters with feedback condition across six subjects are shown for both the elbow and wrist joints, individually. Movement durations and peak velocities for elbow flexion movements of 70 deg combined with wrist flexion movements of 40 deg are shown under the four different target conditions. A one-way analysis of variance (ANOVA) did not reveal any statistically significant differences in movement duration (F=.9, p=.5) or peak velocity (F=.6, p=.7) for elbow flexion across conditions. Similarly, no statistically significant differences in movement duration (F=.8, p=.5) or peak velocity (F=.8, p=.5) were found for wrist flexion across all conditions. Although not shown similar results were found for extension movements for both elbow and wrist movements.

Given that there were no significant changes at the individual joints, the relationship between the joints was analyzed. A general description of this relationship was obtained by studying joint angle/angle plots (Fig. 26). In Fig. 26A, wrist extension movements of 40 deg combined with elbow extension movements of 20 deg are shown for each of the four target conditions. In Fig. 26B, wrist extension movements of 40 deg combined with elbow extension movements of 70 deg, from a different subject are shown. Interestingly, two basic strategies were observed that were dependent on the specific conditions. Movements in the endpoint conditions were characterized by segmented movements of the elbow and wrist joints, i.e in general the wrist joint moved first and was followed by the elbow joint. This was true regardless of the relative amplitudes between the joints. In contrast, a more linear relationship was observed during movements made in response to the segment angle display and during movements made to physical targets, i.e. the elbow and wrist joints tended to move together as a unit.

In order to determine whether peripheral vision of the arm may have influenced these results, the relationship between the joints was examined in the one subject where vision of the arm was blocked during the movements. Fig. 27 shows the angle/angle plots for 70 deg elbow movements combined with 40 deg wrist movements under each of the four conditions, for both flexions and extensions. These plots clearly demonstrate that removing peripheral vision of the arm did not qualitatively influence inter-joint coordination.

Movements made in response to the endpoint conditions were characterized by segmented movements of the wrist and elbow joints. These joints moved as a unit in movements made in response to the physical targets and the segment angle display.

The difference in the two strategies were corroborated by the subjects' perception of the tasks. All seven subjects reported that movements to physical targets and movements in response to the segment angle display were the easiest to perform. The two endpoint display conditions were perceived to be the most difficult. These comments are particularly revealing in light of the fact that most subjects did not realize that they were required to perform the same amplitude movements under the different display conditions.

Figure 25

Kinematic relations of individual elbow and wrist joints across target conditions. Graphs of elbow flexion movement duration and peak velocity (top) and wrist flexion movement duration and peak velocity (bottom) are shown. Each bar is the average obtained from six subjects. Error bars are 1 SEM.

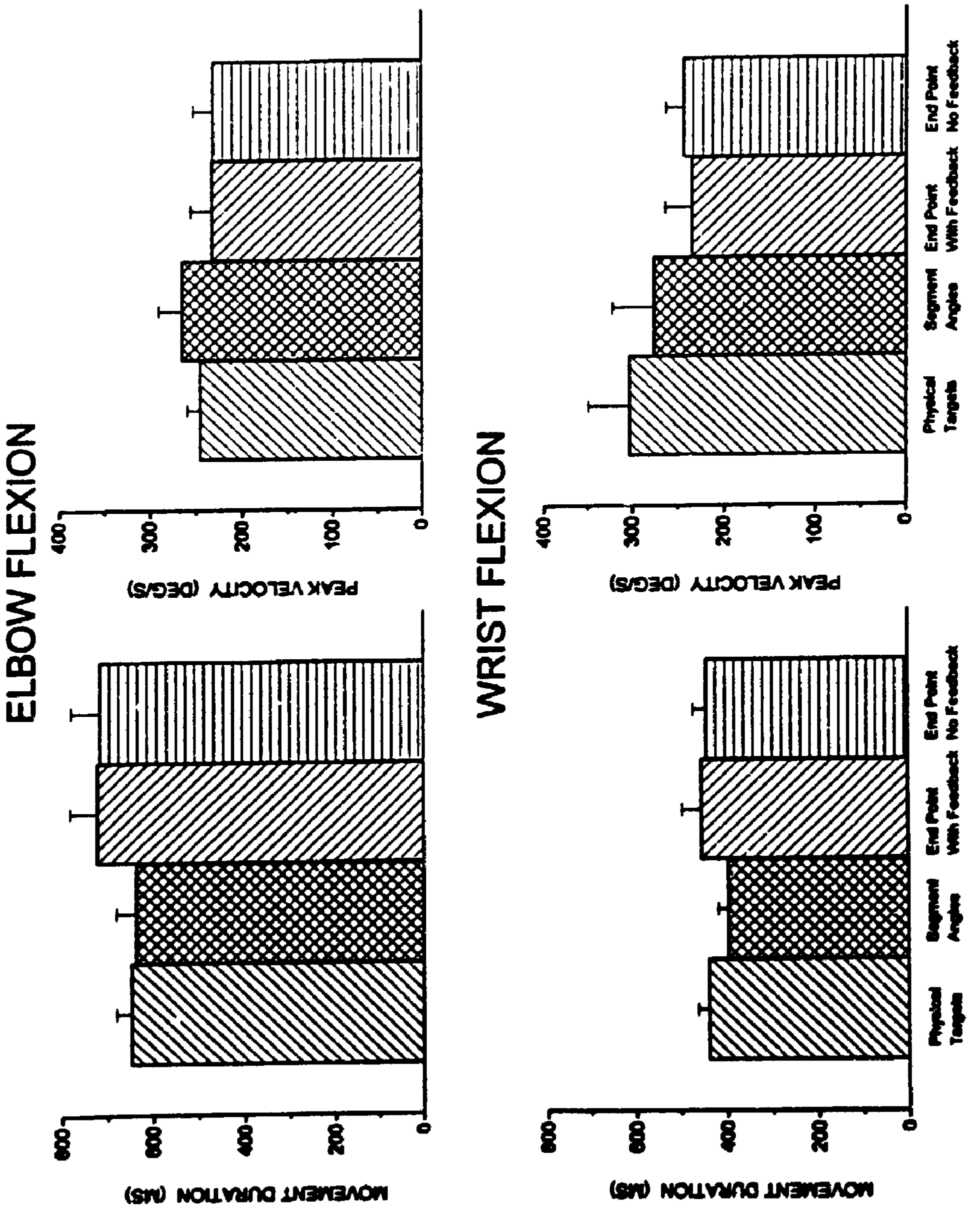

ELBOW FLEXION
MOVEMENT DURATION (MS)
0
200
400
600
800
PEAK VELOCITY (DEG/S)
0
100
200
300
400
WRIST FLEXION
MOVEMENT DURATION (MS)
0
200
400
600
800
PEAK VELOCITY (DEG/S)
0
100
200
300
400
Physical Targets
Segment Angles
End Point With Feedback
End Point No Feedback
Physical Targets
Segment Angles
End Point With Feedback
End Point No Feedback

Figure 26

Joint angle plots for movements made under four target conditions and two movement amplitudes. The relationship between elbow and wrist movements is shown under the four target conditions. In (A) wrist extension and flexion movements of 40 deg were combined with elbow extension and flexion movements of 20 deg, respectively. In (B) wrist extension and flexion movements of 40 deg were combined with elbow extension and flexion movements of 70 deg respectively. Each record is the average of 15 movements. Horizontal calibration represents 20 deg. Vertical calibration in (A) represents 10 deg and in (B), 20 deg.

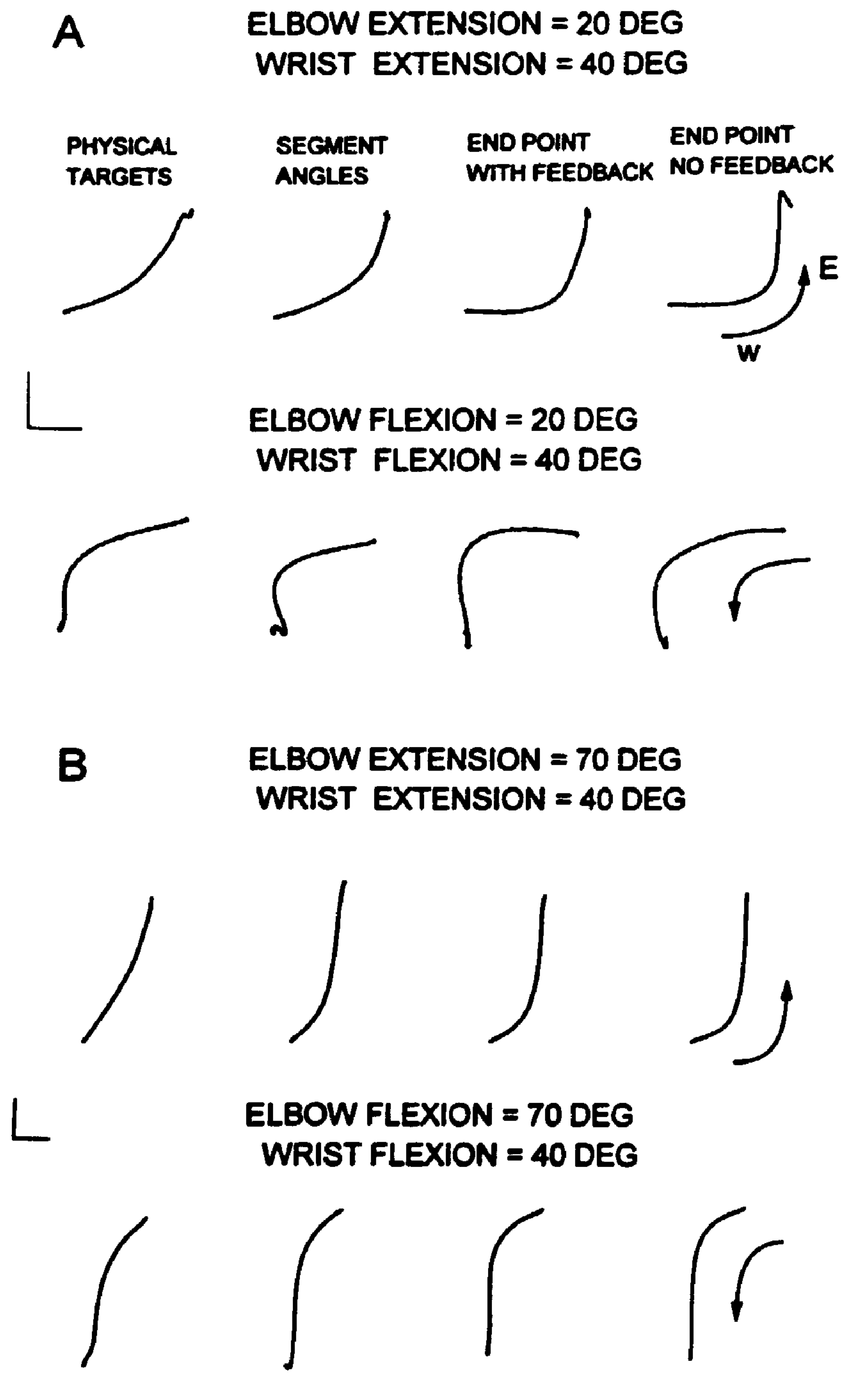
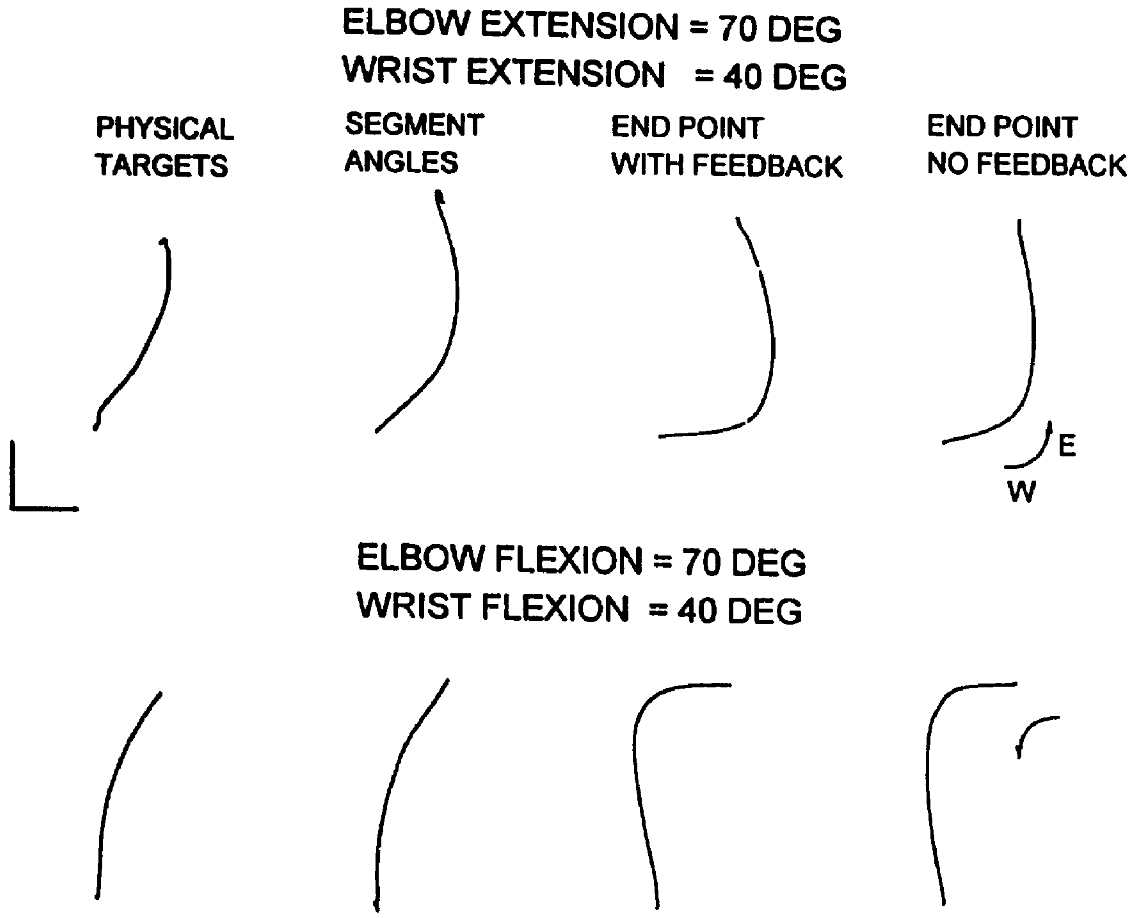

A
ELBOW EXTENSION = 20 DEG
WRIST EXTENSION = 40 DEG
PHYSICAL TARGETS
SEGMENT ANGLES
END POINT WITH FEEDBACK
END POINT NO FEEDBACK
E
W
ELBOW FLEXION = 20 DEG
WRIST FLEXION = 40 DEG
B
ELBOW EXTENSION = 70 DEG
WRIST EXTENSION = 40 DEG
ELBOW FLEXION = 70 DEG
WRIST FLEXION = 40 DEG

Figure 27

Joint angle plots for movements made under four target conditions with vision of the arm blocked. The relationship between elbow and wrist movements is shown under the four target conditions. Wrist extension and flexion movements of 40 deg were combined with elbow extension and flexion movements of 70 deg, respectively. Each record is the average of 15 movements. Horizontal calibration represents 27 deg. Vertical calibration represents 22 deg.

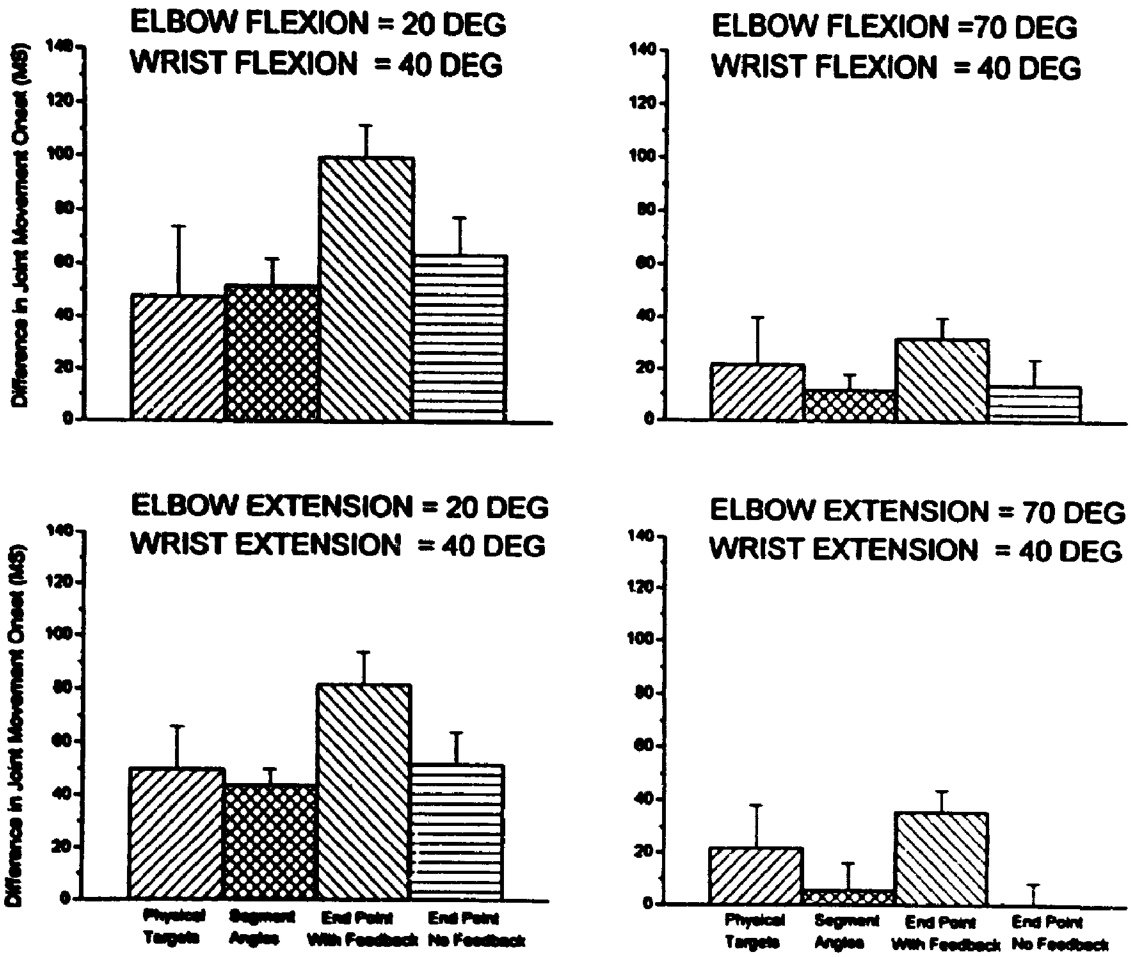

ELBOW EXTENSION = 70 DEG
WRIST EXTENSION = 40 DEG
PHYSICAL TARGETS
SEGMENT ANGLES
END POINT WITH FEEDBACK
END POINT NO FEEDBACK
E
W
ELBOW FLEXION = 70 DEG
WRIST FLEXION = 40 DEG

In order to substantiate these qualitative observations, the difference between the onset times of wrist and elbow movement during both flexion and extension movements across all six subjects was analyzed. In Fig. 28 the average time difference between elbow and wrist movements onsets are shown for all four target conditions and the two movement amplitude conditions for both flexion and extension movements. Positive values indicate that wrist movement started before the elbow movement. On average, in all conditions, wrist movement preceded elbow movement onset. This difference decreased for the larger amplitude elbow movements (see right hand panels). In fact, in a number of subjects elbow movement onset preceded wrist movement onset during the larger amplitude elbow movement condition. For wrist movements of 40 deg combined with elbow movements of 20 deg, the largest difference in joint movement onset was in the endpoint with feedback condition (see left hand panels). The mean onset difference was 100 (+/- 12) ms for flexion movements and 82 (+/- 12) ms for extension movements. The smallest difference in joint movement onset was in the physical target condition for flexion movements (48(+/-26) ms). For extension movements the smallest difference was in the segment angle condition (44(+/-6) ms). In spite of these differences a one-way ANOVA did not reveal any statistically significant differences in joint movement onset times across conditions for either flexion (F=2.2, p=.1) or extension (F=1.8, p=.2) movements.

For wrist movements combined with larger elbow amplitude movements (graph on the right of figure), similar results were observed. The largest difference in joint

Figure 28

Differences in movement onset between the elbow and wrist joints. Average time difference between the elbow and wrist flexion and extension movement onset across four target conditions and two movement amplitudes are shown. Each bar represents data from six subjects. Error bars are 1 SEM.



ELBOW FLEXION = 20 DEG
WRIST FLEXION = 40 DEG
ELBOW FLEXION =70 DEG
WRIST FLEXION = 40 DEG
ELBOW EXTENSION = 20 DEG
WRIST EXTENSION = 40 DEG
ELBOW EXTENSION = 70 DEG
WRIST EXTENSION = 40 DEG
Difference in Joint Movement Onset (MS)
0
20
40
60
80
100
120
140
Physical Targets
Segment Angles
End Point With Feedback
End Point No Feedback

movement onset was in the endpoint with feedback condition. The mean onset difference was 32 (+/- 8) ms for flexion movements and 36 (+/- 8) ms for extension movements. The smallest onset difference for was in the segment angle condition with a mean onset difference of 12 (+/- 6) ms for flexion movements and 6 (+/- 10 ms) for extension movements. These differences were not statistically significant.

Thus far, the results have shown that the target conditions appeared to have qualitatively influenced the coordination between the two joints. In order to determine if these changes were reflected in the muscle activity, the pattern of EMG activity was studied. In Figs. 29 and 30 records of typical EMG activity from elbow and wrist flexion movements from two different subjects are shown. Fig. 29 shows data from wrist flexion movements of 40 deg combined with elbow flexion movements of 20 deg. It is striking to note the qualitative change in the magnitude of the biceps activity across conditions. Movements made in response to physical targets and to segment angle display are associated with distinct bursts of phasic biceps activity whereas in both the endpoint display conditions there was a noticeable lack of phasic activity in the biceps.

In Fig. 30B a similar pattern of change in biceps activity is shown for wrist flexion movements of 40 deg combined with elbow flexion movements of 70 deg from another subject. It is interesting to note that in both conditions, although there were quite significant changes in the muscle activity, there was little corresponding change in the peak velocity and movement duration of elbow movement across conditions. In terms of wrist activity the changes in relation to target condition are less clear.

Figure 29

Wrist and elbow EMG activity under the four target conditions for elbow flexion movements of 20 deg combined with wrist flexion movements of 40 deg. Averaged position, velocity and EMG activity for elbow and wrist movements are shown. Records are the average of 15 movements. Records were aligned to wrist movement start for averaging. Vertical position and velocity calibration represents 20 deg and 90 deg/sec (elbow), 95 deg/sec (wrist). Horizontal calibration represents 280 ms (elbow) and 3[illegible] ms (wrist).

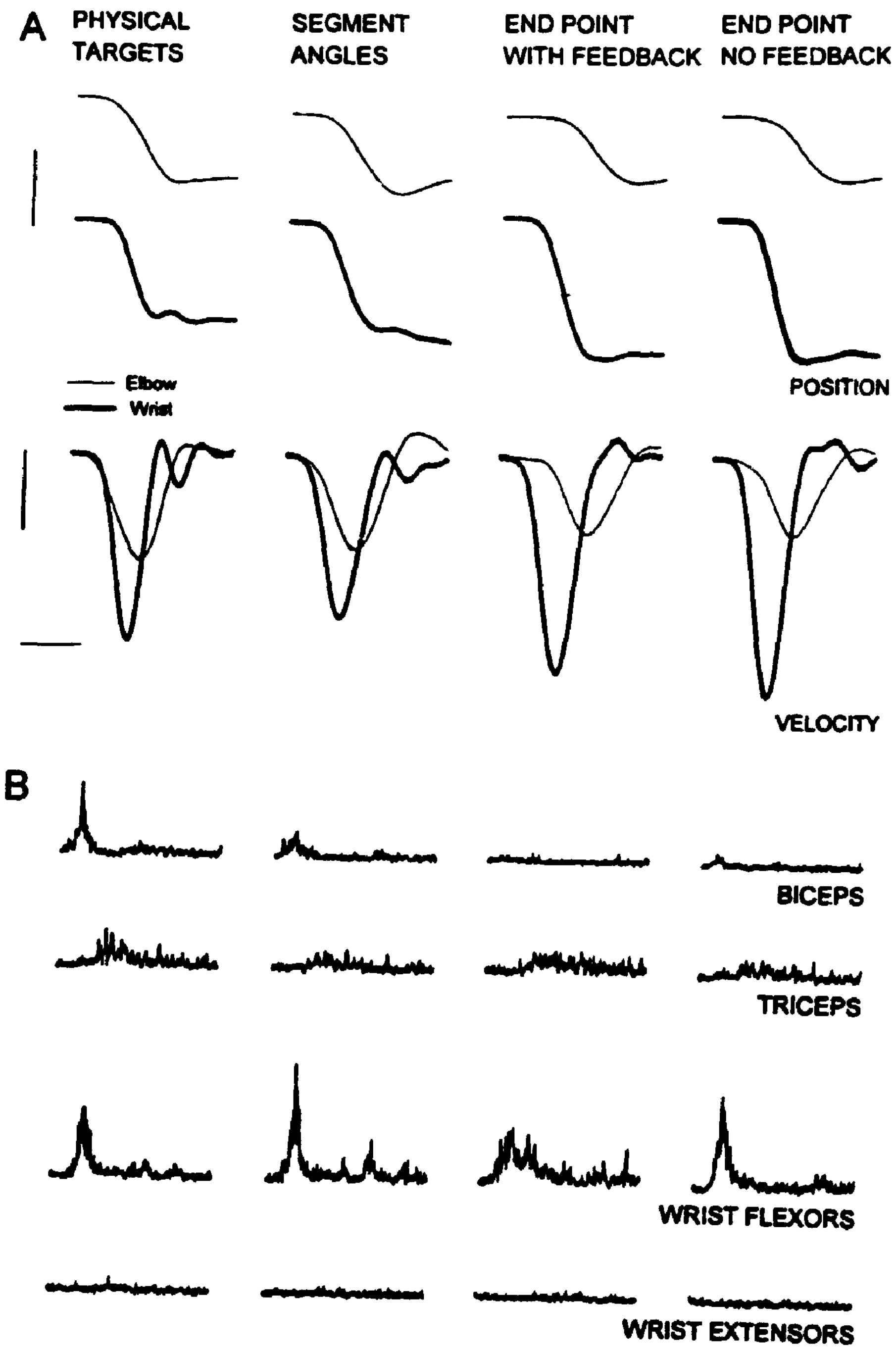
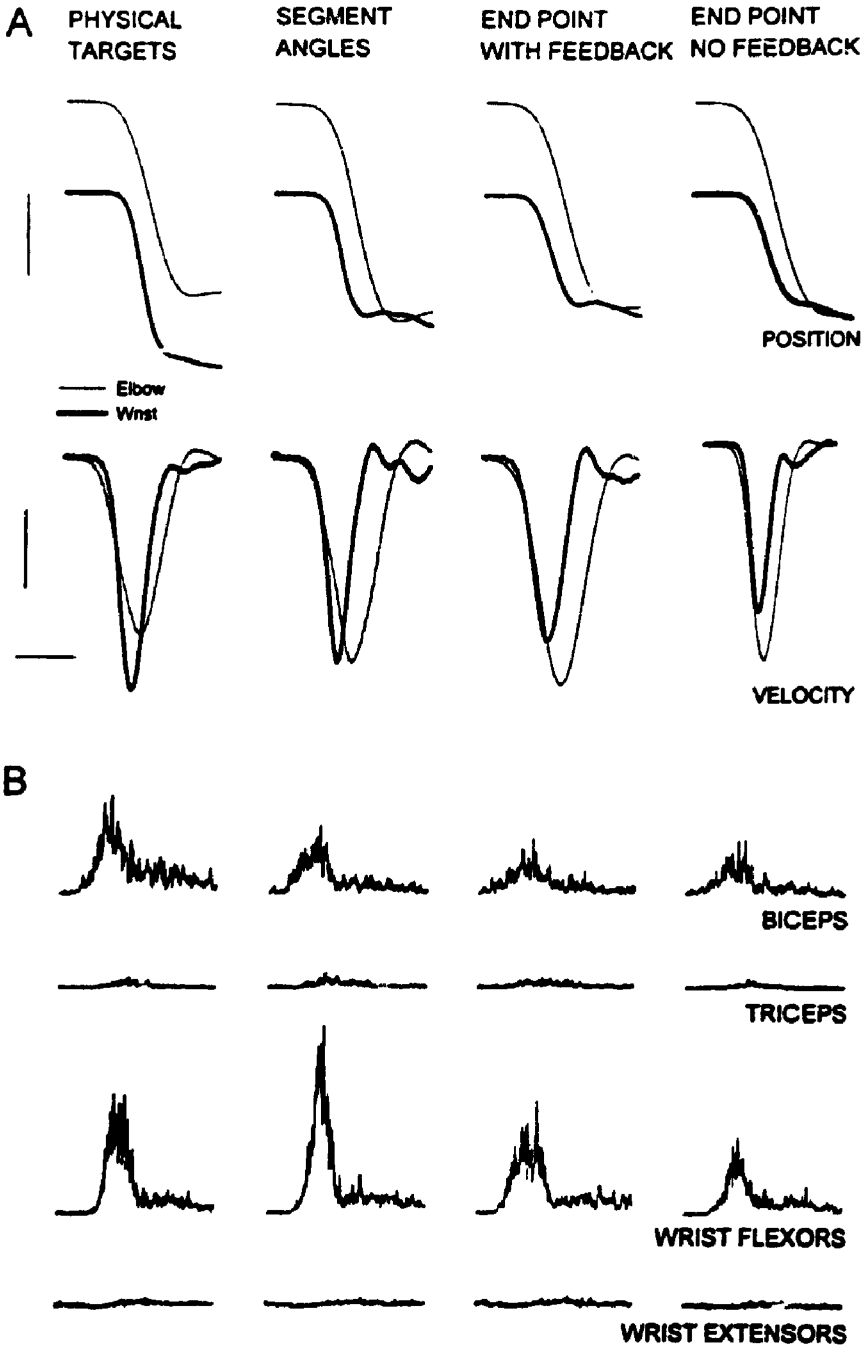

A
PHYSICAL TARGETS
SEGMENT ANGLES
END POINT WITH FEEDBACK
END POINT NO FEEDBACK
Elbow
Wrist
POSITION
VELOCITY
B
BICEPS
TRICEPS
WRIST FLEXORS
WRIST EXTENSORS

Figure 30

Wrist and elbow EMG activity under the four target conditions for elbow flexion movements of 70 deg combined with wrist flexion movements of 40 deg. Averaged position, velocity and EMG activity for elbow and wrist movements are shown. Records are the average of 15 movements. Records were aligned to wrist movement start for averaging. Vertical position and velocity calibration represents 25 deg and 130 deg/sec (elbow), 120 deg/sec (wrist). Horizontal calibration represents 320 ms (elbow) and 360 ms (wrist).


A
PHYSICAL TARGETS
SEGMENT ANGLES
END POINT WITH FEEDBACK
END POINT NO FEEDBACK
Elbow
Wrist
POSITION
VELOCITY
B
BICEPS
TRICEPS
WRIST FLEXORS
WRIST EXTENSORS

In Fig. 29B there appeared to be little qualitative change in phasic wrist flexor activity across conditions. However, in Fig. 30B, qualitatively there was greater phasic wrist flexor activity associated with the physical target and segment angle conditions than in the two endpoint conditions, similar to that observed at the elbow. Again note that the corresponding peak velocity and movement durations are not significantly different.

5.4 Summary

One of the significant findings of this study is that there was little qualitative difference in inter-coordination between movements made in response to the segment angle display (used in the experiments described in Chapters 3 and 4) and pointing movements made to physical targets. The importance of this finding in relation to the experiments discussed in this thesis, is the implication that the segment angle display did not impose unnatural constraints on movement coordination. These movements can therefore be considered to be representative of "normal" movement and the results can be used as a valid platform from which to discuss the general strategies used by the nervous system in movement planning (see Chapter 6).

DISCUSSION

6.1 Introduction

The experiments described in this thesis were undertaken in an attempt to discover the commonalities and differences that exist between the planning of simple, single joint arm movements, and more complex single joint movements as well as multi-joint movements. As such, the influence of gravitational loading in single joint movements was investigated first. In subsequent chapters, multi-joint movements involving rotations about the elbow and wrist joints were analyzed. Finally, the influence of visual feedback information on movement coordination was explored. The purpose of this section is to discuss how the results from each individual experiment have shed some light on specific aspects of motor planning. The relevance of studying single joint movement in order to understand more complex movements will then be considered.

6.2 Effects of gravitational loading on EMG-movement relations

Movements made under different gravitational loading conditions were produced by modulation of a basic muscle activation pattern and were associated with a common movement profile. One of the striking findings of this study was the early phasic antagonist activity which occurred at about the same time as the phasic agonist activity in movements made against gravity. Such early antagonist activity has been previously described (Marsden et al, 1983; Karst and Hasan, 1987; Cooke and Brown,

1990) but is commonly of rather small amplitude as was observed during extension movements made with gravity in this study. It should be noted that the pattern of muscle activation observed in movements against gravity in this study does not correspond with the findings of Cheron and Godaux (1986) who reported a characteristic 'triphasic' EMG pattern for flexion movements made against gravity. Since they presented no kinematic data, it is difficult to interpret their findings within the context of the present study.

In attempting to understand the role of this early antagonist activity a number of hypotheses can be considered. One possibility arises when considering the forces acting at the joint during rapid rotation. As the limb moves from one position to another, there is a tendency for the articulating surfaces of the joint to separate as a result of centrifugal forces. A centripetal force is necessary to counteract this force and can be provided either passively by ligaments or by active muscle contraction. Karst and Hasan (1987) have proposed that the antagonist may play a role in this function. They found that during the performance of inertially loaded forearm movements in the horizontal plane, antagonist activity was greater than that required simply for stopping the movement. In addition, many subjects exhibited coactivation of the agonist and antagonist at the end of these movements. They suggested that "excess" antagonist activity, in conjunction with agonist activity, may serve to provide the force necessary to maintain joint congruency, particular at high velocities. This hypothesis could be extended to the present set of experiments when considering the loads acting at the joint. It is possible that the large torques generated by the muscles to accelerate the limb, in a direction opposing the gravitational torque, increase the likelihood of compromising the joint surface. Coactivation prior to movement onset may be an anticipatory response to prevent this from occurring.

Hogan (1984) hypothesized that the CNS controls the activity of the musculoskeletal system by modulating the mechanical impedance of muscle. Using mathematical modelling and experimental manipulation of static arm positions he showed that when the limb is subjected to destabilizing gravitational torques, the CNS increases joint stability through cocontraction. In the present set of experiments, the magnitude of the gravitational torque at the start of movements, with and against gravity, was approximately the same. However, it is possible that when the limb moves in the same direction as the "destabilizing" force, there is no need to increase stability at the joint. The limb moves in the direction of the gravitational force partly through generation of active force, and to some extent by succumbing to the "destabilizing" force. Thus, the force generated by the muscle prior to movement start is relatively small and is reflected in the relatively small change in AG1 duration. In movements against gravity, the situation is more complex. Not only must the CNS generate adequate muscle activity to initiate movement, but it must also ensure that in generating large forces, the limb is not subjected to unwanted perturbations (Lestienne, et al, 1981). Thus, in this case, the role of the agonist is not simply to regulate acceleration, but in addition, to act with the antagonist to increase joint stiffness, creating a stable base from which to begin movement.

This study has shown that the CNS modulates a basic pattern of activation by taking advantage of external forces. It would appear that in planning and coordinating movement, the CNS not only exploits the passive, interactive and mechanical properties of the system (Bernstein, 1967) but also utilizes the various "resources" available in the environment in which the action takes place.

6.3 Influence of interactional torques on wrist movement during two-joint arm movements in the same direction

One of the primary unresolved issues in multi-joint movement control is the identification of the coordinates in which movements are represented. In attempting to resolve this issue most investigators have focused their analysis either on movement kinematics of the hand or the kinematic relationship between joints. Many early studies reported straight line hand paths and bell-shaped hand velocity profiles during movement, providing evidence for endpoint control (Morasso, 1981; Abend, Bizzi and Morasso, 1982). The implication underlying this strategy is that hand trajectories would be transformed into joint rotations, and the required joint torques derived by inverse kinematic transformations (Hollerbach, 1990). More recently, Atkeson and Hollerbach (1985) proposed a planning strategy based on staggered joint interpolation, i.e. the time at which joints start or stop moving may be staggered with respect to each other, with a common movement profile observed at all joints. This strategy was thought to be more advantageous in that it required less complex, direct kinematic transformations (Hollerbach, 1990). Although there has been some experimental evidence to support this hypothesis (Kaminski and

Gentile, 1986, 1989), the mechanisms by which joint movement onsets may be regulated remain very unclear.

One obvious assumption is that if the CNS was in some manner, actively shifting joint onset times, this would be reflected in the onset times of agonist muscle activity. However, the results from the experiments in Chapter 3 do not support this assumption. Rather, these results show that timing differences between the onset times of elbow and wrist movements were not accompanied by corresponding changes in the onsets of elbow and wrist EMG. This finding is similar to that reported by Karst and Hasan (1991) who showed that no significant correlation existed between the difference in agonist onsets and joint movement onsets for two-joint shoulder and elbow movements. It should be further noted that the relative timings of agonist onsets remained unchanged across the various movement conditions used in this experiment. Although the possibility that changes in AG1 onset may have occurred in other muscles that were not recorded in this study must be considered, the analysis undertaken in this study suggests that the observed changes in joint movement onsets can be explained simply on the basis of joint interactional effects.

As mentioned previously, the actual trajectory of the wrist movement was influenced both by the wrist muscle torques as well as the reaction torques arising from movement about the elbow. The interaction between these torques also affected the timing of wrist movement onset. In conditions where the elbow amplitude was quite small, the magnitude of the wrist muscle torque was larger than the magnitude of the elbow reaction torque and thus wrist movement started at about the same time, or followed shortly after elbow movement onset. At larger elbow amplitudes (i.e. 70 deg), the wrist muscle torque and reaction torque acting at the wrist were equal and opposite in magnitude at the start of movement. As a result, wrist movement onset occurred much later, at a point where muscle torque started to exceed the reaction torque. Thus the relative timing of joint movement onsets was influenced by interactional torques and not directly determined by the CNS.

In terms of agonist onset timing there are two factors that must be considered in multi-joint movement planning. One is the determination of which joint to activate first. This decision may be made on the basis of the relative inertia of individual segments or possibly the relative amplitudes of the movements about the two joints. Once movement about the first joint has been initiated, the onset of movement at the second joint may be determined on the basis of movement direction (Karst and Hasan, 1991; Wadman et al, 1980), or more simply on the direction of desired joint rotation (taking into account the muscle and interactional torques). The location of the target may then determine the selection of the initial muscle activity (Koshland and Hasan,1994).

Once the timing has been resolved, how does the CNS select a particular level of activity (for any particular joint) that is sufficient to produce movements of the same amplitude, regardless of movements about the second joint? It is quite possible that this selection is based on an internal dynamic model of the limb in which basic EMG-movement and kinetic relationships are represented for both single and multi-joint movements. Modifications to basic patterns may then be made according to the specific task or movements being made. Hong et al (1994) have recently shown that the relationship between the EMG muscle activation patterns and torque during a two joint movement involving the shoulder and elbow is similar to that observed in movements about a single joint. In the present task for example, larger movement amplitudes were associated, qualitatively, with increases in AG1 magnitude at both the elbow and wrist joints and basic patterns of muscle activation were observed that were similar to those observed in single joint movements. The difference in these movements was that in the case of wrist movements, qualitatively similar patterns of muscle activity could be associated with movements of different movement durations and magnitudes of peak velocity, though the overall time symmetric structure of the movement remained the same. However, the results from this experiment revealed that these observed kinematic differences could be directly attributed to joint interactional effects. It is interesting to note that the CNS did not counteract elbow reaction torques in order to maintain an identical trajectory for wrist movements of the same amplitude, particularly since this was a striking finding in the experiments described in Chapter 2. Rather, a common pattern of muscle activity was employed for all wrist movements of the same amplitude regardless of elbow amplitude.

It should be pointed out that our present results may be directly influenced by the constraints imposed by the task itself. Although no specific requirements were made regards to the speed or accuracy, the paradigm used in this study did force subjects to focus on individual joint angles as opposed to the endpoint target. However, the consistency of our results with those of other studies that used endpoint targets (Karst and Hasan, 1991; Wadman et al, 1980) suggests that reflects a common planning strategy. It is quite possible that as tasks become more complex, the external requirements may influence planning strategies to a greater extent. Nonetheless, these results indicate that in moving from single joint movements to movements about two joints where the task requirements are relatively simple, the CNS is less concerned about maintaining specific movement characteristics. Thus, it appears that the CNS plans movements only very globally at the joint level, and that the actual trajectory of the movement is not planned but emerges as a result of the integration of basic patterns of muscle activity with the dynamic interactions between joints.

6.4 Influence of interactional torques on wrist movement during two-joint arm movements in the opposite direction

Analysis of the relationship between movement kinematics and the underlying muscle activation pattern has long been a basic approach in understanding how the nervous system formulates motor commands to produce movement. Components of the triphasic pattern, typically observed in planar movements about a single joint (Brown and Cooke, 1981; Hallett et al, 1975, Mustard and Lee, 1987), are well correlated with explicit kinematic variables (Benecke et al, 1985; Berardelli et al, 1984; Brown and Cooke, 1981; 1990, Cooke and Brown, 1994). Such relationships however, have not proved to be as direct in more complex movements. For example, single joint movements made under different loading conditions are associated with quite distinct patterns of muscle activity, although the movement trajectories are remarkably alike (Stein et al, 1988). A number of modifications have also been observed in the EMG-movement relations in multi-joint movements in comparison with the relations observed in planar, single joint movements. For example, the magnitude of the initial agonist burst (Wadman et al, 1980), the time of onset of muscle activity (Flanders, 1991) and the selection of muscle activity (Koshland and Hasan, 1994) are thought to be dependent on movement direction. In addition, the initial muscle activity does not always correspond to the direction of joint rotation (Karst and Hasan, 1991). These observed modifications are in general, related to the force specifications of the task and are less directly associated with specific kinematic variables.

The experiments described in Chapters 3 and 4 have provided additional information about the nature of the modifications required in making two-joint planar movements. Taken together, these findings are significant in that they demonstrate that during two-joint planar movements, a systematic relationship exists between the force specifications of the task and the selection of muscle activation patterns used to produce movement of the distal joint. In conditions where motion of the proximal joint produces torques opposing movement of the distal joint, initial phasic activation is required in the wrist muscle normally termed the agonist. The magnitude of this activity would be dependent on the magnitude of the reaction torques, so that very large reaction torques opposing movement are counteracted by increasing phasic activity. In conditions where motion of the proximal joint produces torques assisting movement of the distal joint, the selection of the muscle to be activated first is again dependent on the magnitude of the reaction torques. Initial phasic activity in the muscle generally termed as the antagonist, would be required to compensate for large reaction torques in order to prevent excessively large movements from occurring.

Interestingly, the pattern of muscle activation selected did not serve to preserve specific kinematic characteristics of the distal joint. Although wrist motion was generally characterized by a bell-shaped velocity profile, the wrist trajectory in general became more variable and less time symmetric as the elbow amplitude increased and the resulting reaction torques became larger in magnitude. Variability in wrist motion has been observed during other multi-joint movements, and it has been proposed that wrist motion may not be linked to movement of the proximal joints and may, in fact, be controlled independently from the more proximal joints (Lacquaniti and Soechting, 1982; Soechting, 1984). However, similar kinematic changes have been reported at the elbow during two-joint movements involving the shoulder and elbow joints (Kaminski and Gentile, 1989) suggesting that this may be a common feature characterising motion of the distal joint.

Based on the results of the two experiments described in Chapters 3 and 4, it appears that wrist motion is linked very closely with elbow motion. The selection of muscle activation patterns at the wrist appears not to be simply dependent on target direction, but on the relative magnitude and direction of the elbow reaction torques in relation to the desired wrist motion. These findings indicate that motion of the elbow joint is an important consideration in planning wrist movements. Thus, movements of the distal joint may be planned very globally at the kinematic level with the variables of primary importance related to the net forces acting at the wrist joint.

6.5 Changes in inter-joint coordination as a result of visual feedback information

It is generally accepted that in bringing the arm to a target, the CNS uses information about target location as well as the initial position of the arm, to generate the appropriate motor commands (Soechting and Flanders, 1991). What is less well known are the steps involved in these transformations, as well as the factors that may influence the specific visuo-motor transformations. The purpose of the experiment described in Chapter 5 was to determine how the attributes of the visual feedback information influence coordination during a two-joint planar movement, involving the elbow and wrist joints. It is important to note that in this task, the initial and final target locations, as well as the initial and final arm configurations were always kept constant. Thus, only the visual feedback display *representing* the target, as well as the arm position was altered. As such, the results of this study are quite interesting.

Essentially, the visual feedback conditions did not affect kinematic relations such as movement durations and peak velocities at the individual wrist and elbow joints. However, these conditions did in fact affect inter-joint coordination. Abstract representations, in which the both the target and the subject's arm were displayed simply as endpoints (with or without feedback about the resulting handpath), resulted in segmented motion in which the wrist joint moved first, followed by the elbow joint. In contrast, movements made in response to more concrete visual representations such as the segment angle display, as well as to actual physical targets, resulted in coordinated movements in which the timing of movement at the two joints were closely related.

In a related experiment, Ghez et al (1995) have recently shown that in deafferented patients, feedback of hand position provided by a screen cursor, or actual viewing of the limb itself, are both equally useful in improving movement accuracy. The authors propose that such improvements are facilitated by visual input which serves to update an internal model of the physical properties of the limb. Unfortunately, the effects of the different visual inputs on movement coordination was not analyzed in these experiments.

In keeping with above hypothesis, the findings from the experiments in Chapter 5 are significant in that they demonstrate that visual input may be necessary for updating internal models even in normal subjects with intact limb proprioception. Indeed, the calibration of such models are subtly influenced by the nature of the available visual feedback information. While abstract limb representations, in the form of endpoints, are sufficient to ensure movement accuracy, such displays do not appear to provide adequate information to assure efficient coordination between joints. This suggests that the nervous system may require some minimum visual information regarding the properties of moving segments in order to coordinate the respective segments.

What then are the implications of these results in understanding how movements are organized? It has been suggested that movement planning must be represented at different levels within the CNS (Atkeson and Hollerbach, 1985; Soechting and Flanders, 1991). At some level, a plan based on movement kinematics may exist, that is organized simply on the basis of target location and the initial arm configuration. At another level, the physical properties of the limb may be represented in a very general form. This general approximation may then be adapted in response to a number of variables that include the dynamic requirements of the task, the properties of the muscles, as well as the characteristics of the external environment. Together, these factors would then determine the pattern of the underlying motor commands.

One of the limitations of this study is that both the limb as well as the target representation were both manipulated. As mentioned previously the paradigm was designed explicitly in this manner to maintain a consistency with the previous experiments. This does raise the possibility however, that abstraction of the target may have influenced the results. Future studies in which the target representation remains fixed while the limb representation is altered, will provide further insights into the role of visual feedback information in movement coordination.

6.6 Can the problem of understanding complex limb movements be solved by understanding the control of single joint movements?

The results from the experiments discussed in this thesis suggest that the study of single joint movements has been useful in so far as providing a basic framework from which broader insights into the nature of complex movements can be developed. The traditional approach of describing the relationship between isolated kinematic variables, as well as the underlying phasic muscle activity, has been found to be rather restrictive and of limited value in understanding the planning of single joint movements. As such, this approach cannot simply be extrapolated to the study of complex movements. Current approaches, however, that have emphasized the importance of integrating kinematic, muscle activity as well as kinetic parameters (Cooke and Brown, 1990, 1994; Ghez and Gordon, 1987; Hoffman and Strick, 1986, 1990; Gottlieb et al, 1989) have paved the way for generating a more complete understanding of complex movements.

It should be noted, however, that the emphasis of many of these approaches remains focused on explaining *kinematic* regularities generally observed in single joint movements. Certainly, there is no doubt that time symmetric velocity profiles as well as the consistent peak velocity and movement duration relations under transformations of movement speed and amplitude, are robust findings in many movements. In fact, the experiments in Chapter 2 clearly demonstrate how modification of muscle activity under different gravitational loads, remains correlated with a common movement trajectory. The question of importance however is: *does the observance of consistent relationships in certain measured variables necessarily imply that those variables are under direct control, and that they reflect global planning strategies?* Not necessarily. It is possible that such relationships may be the consequences of the nervous system's attempt to adhere to more fundamental principles such as minimization of energy or work (Nelson, 1983). Certainly the results from the experiments in Chapters 3 and 4 demonstrate that the pattern of muscle activity is either maintained or modified only to the extent required to reach the target. This is particularly evident in movements of the distal joint, where it is clear that the CNS is less concerned about maintaining or producing invariant trajectories. Rather, the basic alternating pattern of agonist/antagonist activation is modulated in relation to the force requirements of the task to achieve the desired movement. This often results in quite variable trajectories as was observed in the experiments described in Chapter 4.

Interestingly, the final trajectory, particularly at the distal joint, is shaped by the interaction of the sum of the torques acting at that joint. This finding clearly indicates that the CNS does not produce multi-joint movements by independently controlling individual single joints in the linkage (Hasan, 1991). Rather, a more complex process is involved in which the effects of forces from the external environment, as well as the effects of torques from other moving joints are integrated and accounted for only to the extent necessary to achieve the desired result. Thus, adding an additional segment to the linkage, eg. the shoulder joint, would most likely produce significant alterations in the dynamics of the movement and in turn, the muscle activation pattern at the wrist and elbow joints as well as the shape of their movement trajectories.

Does this then imply that single joint movements are controlled in a different manner from multi-joint movements, or that they represent a special case? In planar single joint movements there are no other external forces or interactional torques affecting the movement. Consequently, the muscle activity can be more directly correlated with kinematic variables such as acceleration, since the latter is in fact proportional to the net torque acting at the joint. Thus, even at the single joint level, muscle activity can be correlated with the net torque.

6.7 Implications of current work and future research directions

Do the results of the experiments discussed in this thesis fit with current models of motor control? As has been discussed previously, the staggered joint interpolation model does not adequately explain this data. What is clear from these experiments, however, is that muscle activity is selected on the basis of both the dynamic properties of the limb as well as in response to the external environment or task conditions. A striking example of this is provided by the experiments described in Chapter 2 where there was a an immediate reversal in muscle activation pattern in response to the reversal in the pattern of the gravitational load. The implication of this and the other findings described in this thesis is that the CNS may have a very general, plastic internal model in which estimates of the inertial parameters of the limb such as the mass and moments of inertia are represented (Atkeson, 1989; Lacquaniti et al, 1992; Soechting and Flanders, 1991). As a first approximation, these parameters may be utilized to initially respond to the force requirements of the task. Certainly, inertial parameters in themselves cannot comprise the only parameters of such a model. Properties of the muscle such as length-tension, velocity and stiffness relationships must also be incorporated. In addition, sensory feedback information would be crucial in building and calibrating such a model (Ghez et al, 1995). To date, a complete model incorporating all "relevant" parameters is yet to be developed. This is in part due to the fact that all the controlled parameters have not yet been identified. Future studies that are directed at exploring the influence of task conditions as well as the relative roles of sensory information, particularly during the learning phase of movement may provide valuable insights into the programming of multi-joint movements. In addition, such studies will be useful in uncovering the fundamental principles that the nervous system complies with, in producing both single and multi-joint movements.

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Effects of gravitational forces on single joint arm movements in humans

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Abstract We have examined the kinematics and muscle activation patterns of single joint elbow movements made in the vertical plane. Movements of different amplitudes were performed during a visual, step-tracking task. By adjusting shoulder position, both elbow flexion and extension movements were made under three conditions: (a) in the horizontal plane, (b) in the vertical plane against gravity, and (c) in the vertical plane with gravity. Regardless of the gravitational load, all movements were characterized by time symmetric velocity profiles. In addition, no differences were found in the relationships between movement duration, peak velocity, and movement amplitude in movements with or against gravity. The pattern of muscle activation was influenced however, by the gravitational load. Both flexion and extension movements made with gravity were characterized by a reciprocally organized pattern of muscle activity in which phasic agonist activity was followed by phasic antagonist activity. Flexion and extension movements made against gravity were characterized by early phasic antagonist activity occurring at about the same time as the initial agonist burst. These findings suggest that EMG patterns are modified in order to preserve a common temporal structure in the face of different gravitational loads.

Key words Voluntary movement · Kinematics · EMG Gravitational loading · Human

Introduction

The control strategies used by the CNS in generating skilled movement continues to be one of the fundamental questions in motor control. A major focus of research has been directed towards describing the relationship between specific kinematic variables and the underlying muscle activation patterns in order to identify regularities in the coordination of limb movement. To this end, many studies in the past have been restricted to single joint movements in the horizontal plane. Such movements, however, comprise only a small part of our 'natural' movement repertoire. Many movements are made in the vertical plane, where a number of complexities arise due to the influence of gravitational forces. For example, the magnitude of the gravitational load does not remain constant but changes with joint angle. Furthermore, gravitational loads pose different demands for the motor system depending on the direction in which the movement is made, i.e., elbow flexions are commonly made against gravity, while elbow extensions are made with gravity. How does the CNS organize such movements and how does this organization compare or relate to the known properties of movements made in the horizontal plane?

Many single joint movements made in the horizontal plane are characterized by a smooth, bell-shaped velocity profile in which the duration of the acceleration and deceleration phases are approximately equal (Ostry et al. 1987). Although the velocity profile may be temporally asymmetric in movements requiring a high degree of accuracy (Soechting 1984; Gentilucci et al. 1991), time symmetric velocity profiles have been reported for many well-learned movements, including single joint movements in the vertical plane (Atkeson and Hollerbach 1985), multijoint movements (Morasso 1981; Soechting 1984; Kaminski and Gentile 1986), speech movements (Ostry 1986) and movements of the vocal folds (Munhall et al. 1985). Time-symmetric velocity profiles have been found to remain consistent under transformations of movement amplitude, duration.

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speed, and load (Morasso 1981; Atkeson and Hollerbach 1985; Ostry et al. 1987; Cooke et al. 1987) leading to the suggestion that this profile may represent a fundamental organizing principle underlying movement through minimization of energy (Nelson 1983), optimization of joint stiffness (Hasan 1986), or minimizing the rate of change of acceleration (i.e., jerk) (Hogan 1984).

How does the nervous system formulate the motor commands to produce movements having a common temporal structure? Movements of different temporal structures have been shown to be produced by modification of a 'triphasic' pattern of muscle activation (Brown and Cooke 1990). Components of the triphasic pattern are highly correlated with specific kinematic parameters. For example, both the magnitude and duration of the initial agonist burst (AG1) increase with movement amplitude (Berardelli et al. 1984; Brown and Cooke 1984; Benecke et al. 1985). How do the EMG-movement relationships observed in horizontal movements compare to movements made under the influence of gravity? To date, few studies have examined both the kinematics and the underlying muscle activation patterns for movements in this plane. Cheron and Godaux (1986) reported that elbow flexion movements made in the vertical plane were characterized by a 'triphasic' pattern of muscle activation, similar to that observed in movements made in the horizontal plane. However, Stein et al. (1988) demonstrated that the pattern of muscle activity was in fact highly influenced by loading conditions. They examined wrist flexion movements performed under elastic, viscous, and inertial loads. Each loading condition was associated with a specific pattern of muscle activity resulting in the production of quite similar movements. Given the inconsistent data on the effects of gravitational and other loads, our purpose was to examine and compare in more detail, the EMG-movement relationship in single joint movements made in both the horizontal and vertical planes. The data to be presented here demonstrate that regardless of the gravitational load, movements are characterized by time symmetric velocity profiles. This profile is associated with modification of a basic pattern of muscle activation which is dependent on whether movements are performed with or against gravity.

Methods

Experimental paradigm

Eight normal subjects (aged 22–52 years) with no known history of motor system disorders participated in this study. Subjects performed elbow flexion and extension movements in a visual step-tracking paradigm. The subject's forearm position was displayed as a horizontal line on a television monitor placed at eye level 1.8 m in front of the subject. A horizontal target bar displayed on the screen switched at a regular rate (every 5 s) between two fixed vertical positions. Subjects were required to superimpose the position cursor on the target bar and were instructed to move "fast and accurately." By adjusting the shoulder position, elbow flexion and extension movements were made under the following three conditions

Vertical plane: flexion against gravity extension with gravity

Each subject was seated comfortably with the shoulder in 0 deg abduction, elbow flexed to 100 deg (full elbow extension = 180 deg), forearm supinated and fingers lightly flexed. Movements of five different amplitudes (5,10,20,30, and 40 deg) were performed from this starting position. At each amplitude a block of 30 movements consisting of 15 flexion and 15 extension movements was performed. Presentation of each new block was preceded by a rest period of 2–3 min. Several practice movements were made at each amplitude prior to data collection

Vertical plane: flexion with gravity extension against gravity

In three subjects the direction of the gravitational load was reversed. Each subject was seated with the shoulder flexed to 180 deg, elbow flexed to 100 deg, forearm supinated, and fingers lightly flexed. In this position, 30 deg elbow flexion movements were made with gravity while extension movements were made against gravity. Each experimental session consisted of two blocks of movements, each block consisting of a total of 15 movements (eight flexion and seven extension). The number of trials in each block was reduced in this condition in order to reduce fatigue resulting from maintaining the shoulder in this position for prolonged periods of time

Horizontal plane

Each subject was seated comfortably and grasped a vertical rod attached to a manipulandum which rotated in the horizontal plane about a vertical axis. The subject's shoulder was abducted to 90 deg with the elbow flexed to 100 deg and supported beneath the pivot point. Thirty elbow movements at an amplitude of 20 deg were performed in this position.

Data recording

Angular positions for movements made in the vertical plane were obtained using an electrogoniometer (Penny and Giles). For movements in the horizontal plane, the angular position of the manipulandum (and thus the elbow joint) was measured with a precision potentiometer. Surface EMGs were recorded from the biceps and lateral head of triceps brachii with Ag-AgCl electrodes (0.8 cm in diameter) placed longitudinally about 3 cm apart over the muscle bellies. EMGs were filtered (10–1000 Hz bandpass) and full wave rectified prior to digitization. For movements made in the horizontal plane, angular position was obtained from a precision potentiometer. The data were digitized on-line at 500 Hz and stored for later off-line analysis.

Data analysis

Kinematic data were smoothed by digital filtering (30 Hz, zero phase shift) prior to analysis. Velocity and acceleration were obtained from individual flexion and extension movements by differentiation of the position signal. The times of the start and end of acceleration and deceleration were determined using a threshold of 120 deg/s^2. These times were used in determining movement duration, peak velocity and symmetry ratio (i.e., the ratio of acceleration duration to deceleration duration). Mean values for peak velocity, movement duration and acceleration deceleration duration ratios from each subject were used to calculate the means and standard deviations across all subjects, at each amplitude. Onset and offset times of EMG bursts were determined using interactive

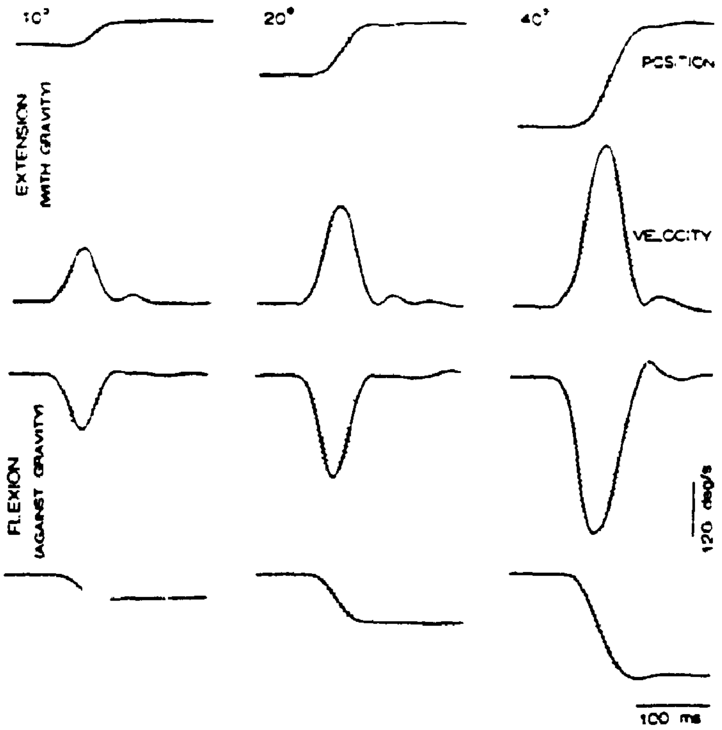


Fig. 1 Movements made with and against gravity. Records of position and velocity from extension (with gravity *upper set*) and flexion (against gravity *lower set*) are shown for movements of three amplitudes (10 20. and 40 deg) Each record is the average of 15 movements *Dashed lines* indicate ± 1 SD Records were aligned to movement start for averaging

graphics Only those records in which EMG onset and offsets could be clearly identified were used for analysis. As a result records from only three subjects were used in this analysis (shown in Fig. 6)

Moments of force

Since the EMG activity must, in some way, reflect the force output of the muscles, we analyzed the torques acting on the limb using the following equation governing the motion of a single segment:

$I\alpha = Tm - mgr\cos\theta$

where
I = moment of inertia of the segment, α = angular acceleration, Tm = moment of force (torque) due to muscle activity, m = mass of the segment (forearm plus hand), g = gravitational acceleration, r = distance from center of gravity to the pivot point, θ = segment angle

This equation can also be written as:

$Te = Tm - Tg$

where
Te = net torque resulting in angular acceleration of the limb, Tm = torque due to muscle activity, Tg = torque due to gravitational acceleration

Results

Movement kinematics

Averaged position and velocity records of extension (with gravity) and flexion (against gravity) movements made in the vertical plane by one representative subject are shown in Fig. 1. The characteristic bell-shaped velocity profile was observed at all amplitudes for both flexion and extension movements. In several subjects, extension movements made with gravity did not terminate smoothly and a small period of oscillation was observed at the end of movement. In flexion movements, this was only observed in large amplitude movements.

Changes in kinematic parameters with movement amplitude across six subjects are shown in Fig. 2. Peak velocity increased linearly with movement amplitude for both flexion ($r = 0.99$) and extension ($r = 0.99$) movements (Fig. 2A). There was no significant difference in the slopes ($P = 0.15$). In addition, no significant difference was found in the peak velocities between flexions and extensions at any amplitude (e.g., for 40 deg amp: $P = 0.43$). Figure 2B illustrates the relation between movement duration and movement amplitude. Movement duration increased linearly with movement amplitude for both flexion and extension (flexion $r = 0.97$, extension $r = 0.96$). On average, extension (with gravity) movements appeared to be of shorter duration than flexion (against gravity) movements. However, no signif-

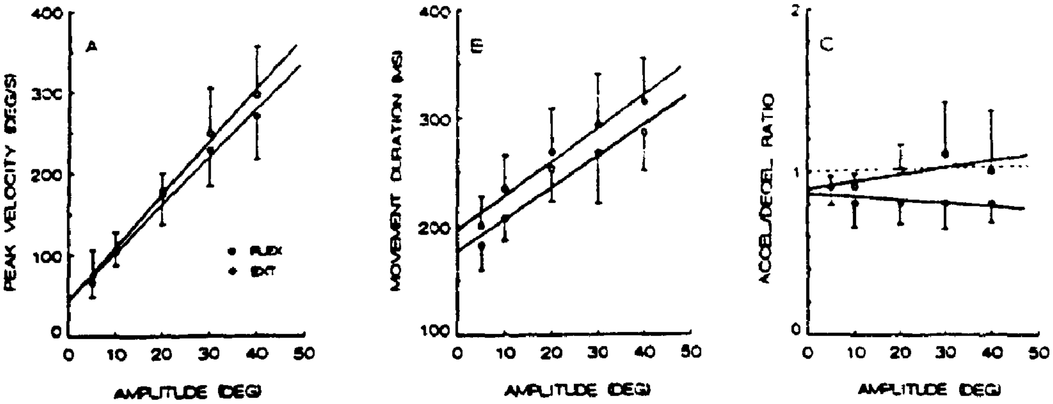


Fig. 2 Kinematic relations Graphs of peak velocity (A), movement duration (B) and the ratio of acceleration to deceleration durations (C) are shown. Each point is the average (±1 SD) obtained from six subjects. *Solid lines* are the best-fit linear regression lines for data from flexions (closed symbols) and extensions (*open symbols*). A Peak velocity amplitude. flexion Vp = 45 + 5.9 A: extension Vp = 44 + 6.5 A. B Movement duration amplitude: flexion MD = 196 + 3.1 A. r = 0.97: extension MD = 177 + 2.9 A. r = 0.96. C Symmetry ratio/amplitude: flexion SR = 0.88–0.003 A. r = 0.71, extension SR = 0.86 + 0.004 A. r = 0.76. The *dashed horizontal line* in C indicates a ratio of 1.0

icant differences were found between the slopes ($P = 0.37$) or between movement durations at any amplitude (for 40 deg amp: $P = 0.23$).

Mean symmetry ratios (acceleration duration deceleration duration) are plotted in Fig. 2C for six subjects. A significant difference was found between the slopes of the two regression lines ($P < 0.05$). For flexion movements there was a trend towards decreasing symmetry ratios as amplitude increased. Symmetry ratios ranged from 0.8 to 0.9 with a mean of 0.82 indicating that, on average, the duration of deceleration was slightly greater than the duration of acceleration for movements made against gravity. Extension movements made with gravity exhibited a trend towards increasing symmetry ratios as amplitude increased. Symmetry ratios ranged from 0.8–1.2, with a mean of 0.9. Statistical analysis, however, revealed a significant difference only for 30 deg movements ($P = 0.006$). This difference may have arisen in part from the data of one particular subject who had consistently larger symmetry ratios for extension and smaller ratios for flexions at the larger amplitudes. If this subject's data were removed, no significant differences remained. In general extension movements were time symmetric at all amplitudes. Flexion movements exhibited slightly asymmetric profiles, with deceleration duration marginally greater than acceleration duration.

In order to further compare flexion and extension movement profiles, averaged velocity records were adjusted for movement duration and peak velocity. Averaged flexion records for each amplitude were used as a reference. The averaged peak velocities and movement durations from extension movements were scaled by an appropriate factor and overplotted on the flexion records. Figure 3 illustrates the velocity profiles from one subject. This figure illustrates an overlap in the velocity profiles between the two different movements at all amplitudes, demonstrating that a common movement profile was produced for movements with and against gravity.

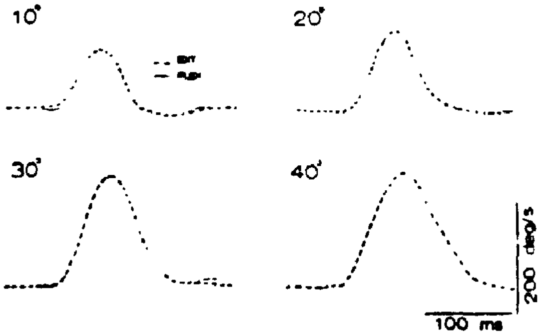


Fig. 3 Scaling of velocity profiles. Averaged velocity records are shown from movements of four amplitudes (10. 20. 30 and 40 deg) made by one subject. Each record is the average of 15 movements At each movement amplitude. the average velocity records from extension movements (*dashed lines*) were scaled to the duration and peak velocity of the corresponding flexion movements (*solid lines*) and inverted for plotting Records were aligned to movement onset for averaging and plotting

Muscle activation patterns/moments of force

Horizontal plane

In Fig. 4 the averaged position, velocity, and associated EMGs are shown for flexion and extension movements made in the horizontal plane. Both flexion and extension movements were time-symmetric and in both, AG1 occurred prior to movement start, providing the driving force to set the limb in motion. Phasic activity in ANT

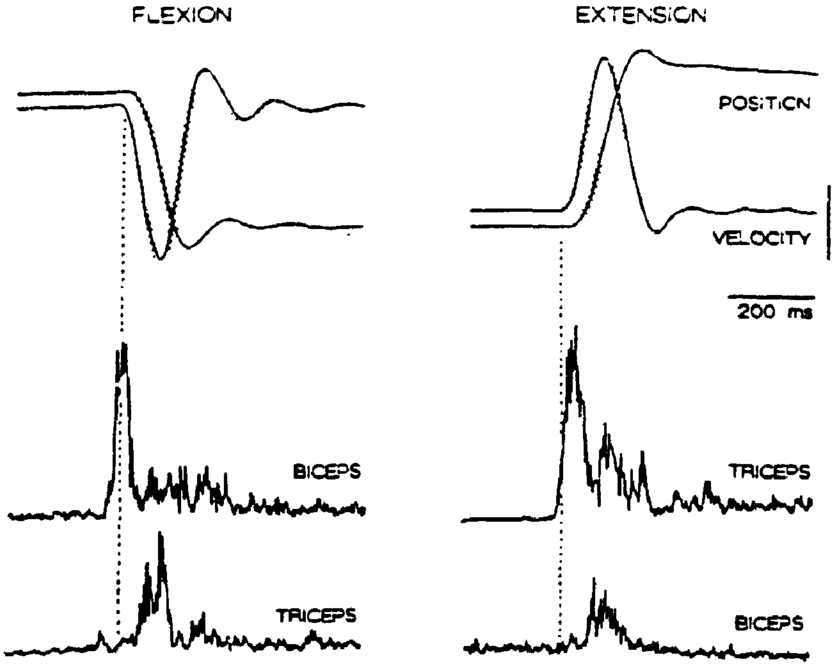


Fig. 4 EMG activity during single joint elbow flexion and extension movements made in the horizontal plane. Averaged position and velocity records from flexion and extension movements in the horizontal plane. Records are the average of 15 movements for 20 deg movements. Records were aligned to movement start for averaging *Dotted line* indicates movement onset. Vertical position and velocity calibration represents 10 deg and 130 deg s respectively

occurred at or near peak velocity and was followed by a second, smaller burst in the agonist (AG2).

Vertical plane-flexion against gravity/extension with gravity

The muscle activation patterns associated with flexion (upper panel) and extension (lower panel) movements made in the vertical plane are illustrated in Fig. 5. Both flexion and extension movements were initiated by AG1 which occurred prior to movement start. The data from this subject shows that AG1 occurred earlier (with respect to movement onset) for movements made with gravity in comparison to movements made against gravity; this was not, however, a consistent finding across all subjects. The most striking difference between flexion and extension movements was related to the time of onset of phasic antagonist activity. For flexion movements made against gravity, phasic antagonist activity started at virtually the same time as AG1. A second antagonist burst followed at about the time of movement peak velocity. In contrast, in extension movements made with gravity, a single antagonist burst occurred later in the movement, near the time of peak velocity.

A linear relationship was observed between AG1 duration and movement amplitude in both flexion and extension movements. However, differences were observed in the slopes of this relation. The data in Fig. 6 represent averaged burst durations taken from individual records from three subjects. For flexion (against gravity) movements the mean burst durations ranged from 57 (±1) ms for 10 deg movements to 112 (±3) ms for 40 deg movements. For extension (with gravity) movements burst durations ranged from 48 (±9) ms for 10 deg movements to 62 (±11) ms for 40 deg movements. Although in both flexion and extension movements AG1 duration increased linearly with movement amplitude (flexion: $r = 0.99$; extension: $r = 0.92$), the slope of the relation was greater in flexion movements. A significant difference was found between the slopes of the two regression lines ($P < 0.001$). The right hand graph in Fig. 6 shows the time of onset of (ANT) relative to the onset of (AG1), for both flexion (against gravity) and extension (with gravity) movements. In flexions, ANT onset occurred on the average, 12 (± 4.6) ms after the onset of AG1. Since the shortest agonist burst duration was 57 (± 1) ms, this indicates that phasic activity in the agonist and antagonist occurred quite close together. In contrast, during extension movements, ANT onset occurred on the average, 91.5 (±22.5) ms after the onset of AG1. The largest mean AG1 burst duration in this case was 62 (±11) ms. Thus, there was little if any AG1-ANT coactivity during extension movements.

Figure 7 shows the torques due to gravity (*Tg*), muscle activity (*Tm*) and the net torque (*Te*) calculated from the averaged data of one representative subject for a movement amplitude of 30 deg. By convention, forearm movement in a counterclockwise direction was considered to be positive and those in a clockwise direction negative. In both flexion (against gravity) and extension (with gravity) movements, the magnitude of the static torque (prior to movement start) due to gravity (*Tg*) was approximately 1.7 Nm, acting in a negative direction to

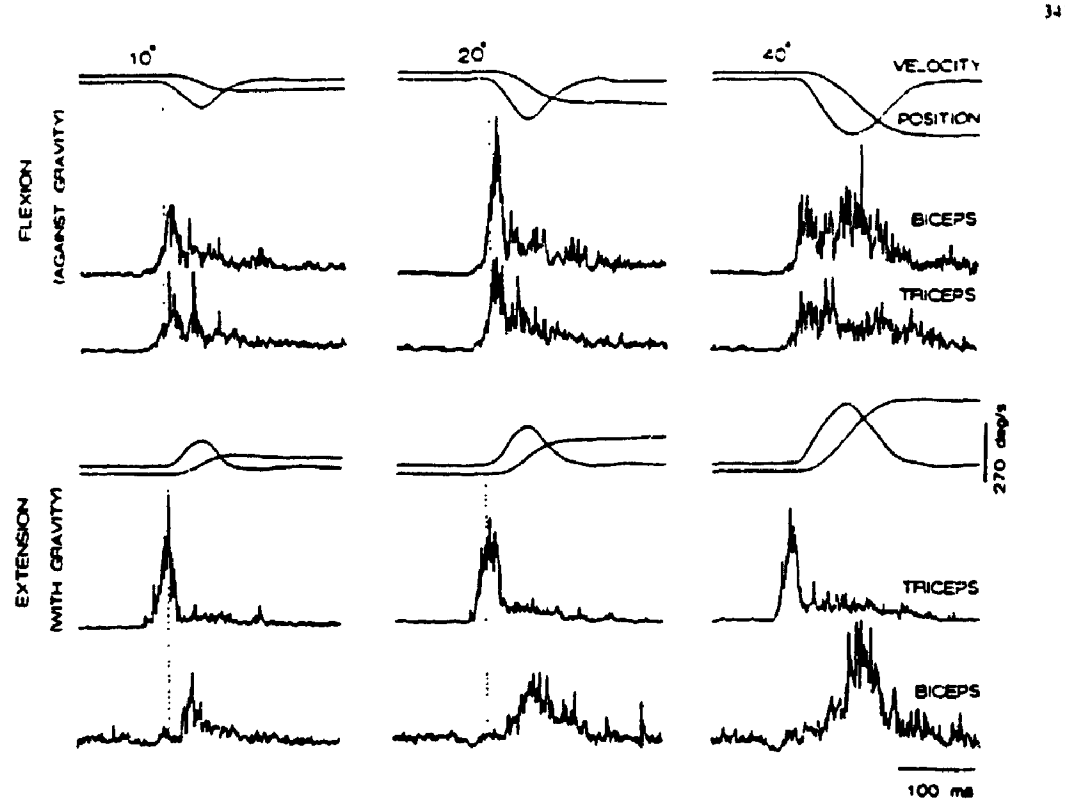
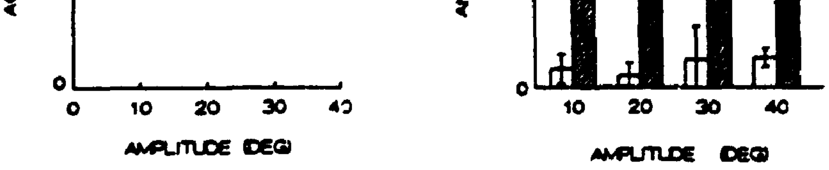


Fig. 5 EMG activity during elbow movements made in the vertical plane. In each set of records are shown averaged position, velocity and EMG activity for movements of three amplitudes (10, 20, and 40 deg). Traces are the average of 15 movements. The *upper set* illustrates flexion (against gravity) movements and the *lower set* illustrates extension (with gravity) movements. Records were aligned to movement start for averaging. *Vertical dotted line* indicates movement onset. It should be noted that the amplitude scale across all panels is constant

Fig. 6 AG1 Duration and onset latency of ANT. The change in AG1 duration with amplitude is shown in the *left hand graph*. Each point is the average (± 1 SD) obtained from three subjects. *Solid lines* are the best-fit linear regression lines for data from flexions (*closed symbols*) and extensions (*open symbols*). The *right hand graph* shows the time span between the onset of AG1 and ANT. Each *bar* is the average (± 1 SD) from three subjects. Flexions are indicated by *open bars* and extensions by *striped bars*



produce a clockwise rotation of the forearm. Note that there was little change in the magnitude of T_g throughout both flexion and extension movements. In flexion (against gravity) movements, T_g was acting in a direction opposite to the intended movement (Fig. 7, left panel). The magnitude of T_m was 1.7 Nm prior to movement start and increased to 2.7 Nm at the time of peak torque. The net change in magnitude and direction of T_m was due to two distinct components. The first was the change in torque needed to overcome the inertial

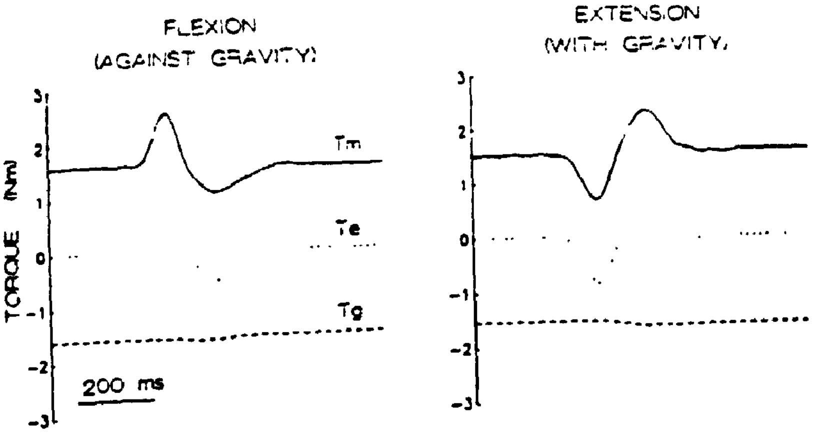


Fig. 7 Calculated torques during movement. Records of the torque due to gravity (*Tg*), torque due to muscle activity (*Tm*) and net torque (*Te*) for flexion (against gravity) and extension (with gravity) movements. Traces are the average of ten movements for 30 deg movements

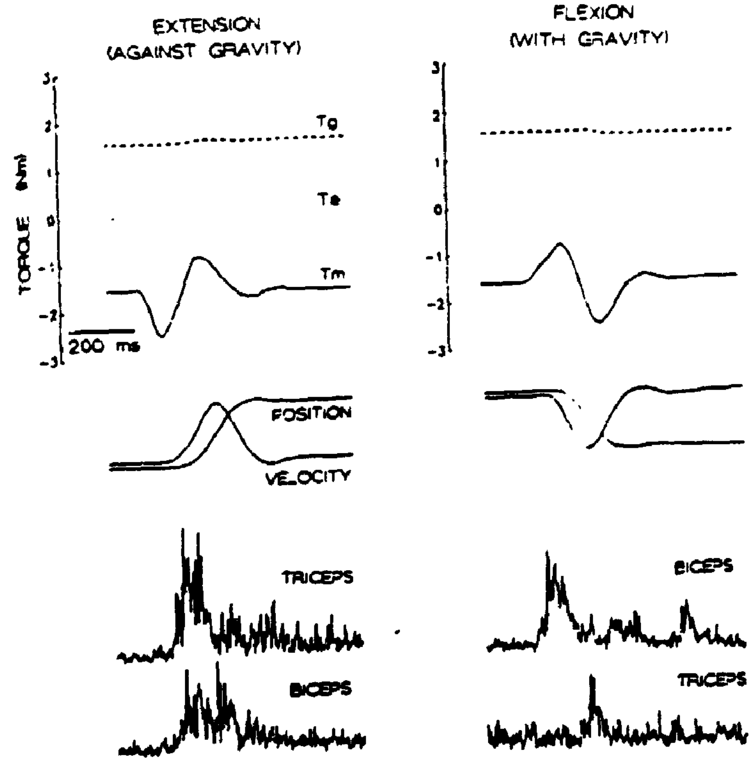


Fig. 8 Torques and EMGs during reversed loading conditions. Records of the torque due to gravity (*Tg*), torque due to muscle activity (*Tm*) and net torque (*Te*) for flexion (with gravity) and extension (against gravity) movements. In each set of records are shown the averaged position, velocity and EMG activity for 30 deg movements. Traces are the average of ten movements. Records were aligned to movement start for averaging

forces: this was proportional to acceleration. The second was the flexor torque required to compensate for *Tg*. Since there was little change in the magnitude of *Tg* during the movement, the component of *Tm* necessary to overcome *Tg* was held approximately constant as movement progressed. That is, the presence of *Tg* served to increase the baseline magnitude of *Tm*. The right panel in Fig. 7 illustrates that in extension movements made with gravity, *Tg* was acting in the same direction as the intended limb movement. The magnitude of *Tm* was 1.5 Nm prior to movement start and decreased to 0.7 Nm at the time of peak torque. Again, the magnitude and direction of *Tm* was based on the torque necessary to overcome the inertial forces and to account for the presence of *Tg*. In this case, however, *Tg* served to assist limb acceleration, resulting in a decrease in the magnitude of *Tm* as the movement progressed. As illustrated, an increase in flexor torque was required to overcome the clockwise torque due to *Tg* and bring the limb to a stop.

Vertical plane-flexion with gravity extension against gravity

The reversal in the pattern of the gravitational load resulted in an appropriate modulation of the muscle activation patterns Figure 8 illustrates the averaged position and velocity records and the torques due to gravity (*Tg*), muscle contraction (*Tm*), and net torque producing angular rotation (*Te*) for flexion (with gravity) and extension (against gravity) movements. The corresponding averaged EMG muscle activation patterns are also shown. In this task *Tg* was acting to produce a positive or counterclockwise rotation of the forearm. Thus in flexion movements made with gravity, *Tg* was acting in the same direction as the limb movement (right hand graph in Fig. 8). A static extensor torque of −1 4 Nm was produced prior to movement start and decreased to −0.8 Nm at the time of peak force. In extension (against gravity) movements. *Tg* was acting in a direction opposite to the intended movement. A static extensor torque of −1.4 Nm was produced prior to movement start and increased to −2.5 Nm at the time of peak acceleration Flexion movements made with gravity exhibited an initial agonist burst followed by phasic activity in the antagonist, similar to that previously observed in extension movements performed with gravity. Extension movements made against gravity showed early, simultaneous phasic muscle activity in both the agonist and antagonist, as had been observed in flexion movements against gravity.

Discussion

Movements made under different gravitational loading conditions were produced by modulation of a basic muscle activation pattern resulting in a common movement profile. This general finding is consistent with that observed by Stein et al. (1988). The studies reported here, however, have demonstrated how the CNS alters the known relationships between phasic muscle activity and specific kinematic parameters, to preserve similar movements under different conditions. For example, subtle differences were apparent in the relationship between AG1 duration and movement amplitude in movements made with gravity. Across a 30 deg range of movement amplitude, AG1 duration increased by 96% in movements made against gravity. This finding is similar to that reported for movements made in the horizontal plane (Berardelli et al. 1984; Brown and Cooke 1984). In contrast, AG1 burst duration increased by only 29% in movements made with gravity, across the same amplitude. Recently, Brown and Cooke (1990) have proposed that changes in AG1 are related not to parameters such as movement amplitude but rather to the temporal characteristics of the movement. They showed, for example, that AG1 duration increases with increasing acceleration duration in movements where both movement amplitude and duration are held constant. AG1, in conjunction with ANT, is thought to regulate the rate of increase and decrease of acceleration In the present task, although the duration of acceleration increased in movements made with and against gravity the influence of gravitational torque on forearm rotation must be taken into account. During extension movements, the torque due to gravitational acceleration acted in the same direction as the movement Hence it is quite possible that the CNS takes advantage of gravitational forces and uses it in combination with muscle activity to produce movement. This would then result in a reduction of the total muscle activity required to accelerate the limb, leading to a relatively small increase in AG1 duration with movement amplitude, compared to movements made against gravity or in the horizontal plane.

Movements made against gravity, although also characterized by time symmetric velocity profiles, were produced by changes in the pattern of phasic muscle activity. Most striking was the phasic antagonist activity which occurred at about the same time as AG1 A second, later burst of antagonist activity commonly occurred. Such early antagonist activity has been previously described (Marsden et al. 1983; Karst and Hasan 1987; Cooke and Brown 1990), but is commonly of rather small amplitude as was observed during extension movements made with gravity in this study It should be noted that the pattern of muscle activation observed in movements against gravity in this study does not correspond with the findings of Cheron and Godaux (1986), who reported a characteristic 'triphasic' EMG pattern for flexion movements made against gravity. Since they presented no kinematic data, it is difficult to interpret their findings within the context of the present study.

In attempting to understand the role of this early antagonist activity it must first be emphasized that the EMG record is, at best, an indirect representation of the total force produced by the muscle (Loeb and Gans 1986). Thus, although the amplitude of the agonist and antagonist appear to be equal, the agonist must have produced greater force for movement to occur Keeping this in mind, a number of hypotheses can be considered. One possibility arises when considering the forces acting at the joint during rapid rotation. As the limb moves from one position to another, there is a tendency for the articulating surfaces of the joint to separate as a result of centrifugal forces. A centripetal force is necessary to counteract this force and can be provided either passively by ligaments or by active muscle contraction. Karst and Hasan (1987) have proposed that the antagonist may play a role in this function. They found that during the performance of inertially loaded forearm movements in the horizontal plane, antagonist activity was greater than that required simply for stopping the movement. In addition, many subjects exhibited coactivation of the agonist and antagonist at the end of these movements. They suggested that 'excess' antagonist activity, in conjunction with agonist activity, may serve to provide the force necessary to maintain joint congruency, particularly at high velocities. This hypothesis could

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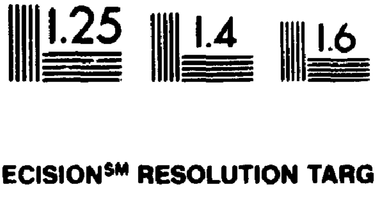

PRECISION℠ RESOLUTION TARGETS

be extended to the present set of experiments when considering the loads acting at the joint. It is possible that the large torques generated by the muscles to accelerate the limb, in a direction opposing the gravitational torque, increase the likelihood of compromising the joint surface. Coactivation prior to movement onset may be an anticipatory response to prevent this from occurring.

An alternative explanation of the early antagonist activity when moving against gravity is related to shoulder stabilisation. Thus, in Fig. 8, biceps acts across the shoulder as well as the elbow. A similar explanation might hold for Fig. 5 (flexions against gravity) if the early triceps activity were due to cross talk from the biceps or the long head of triceps (which also acts across the shoulder). Cross talk from biceps appears quite unlikely since in the extension movements of Fig. 5 there is no triceps activity during the late, large biceps activity. In regards to cross talk from lateral triceps, recordings were made from both lateral and long triceps during the course of these experiments (to be reported elsewhere). In brief, during flexion (against gravity) movements, the long head was barely active during the early burst in the lateral head. Thus, the early antagonist burst does not appear to be related to shoulder stabilisation.

Hogan (1984) hypothesized that the CNS controls the activity of the musculoskeletal system by modulating the mechanical impedance of muscle. Using mathematical modelling and experimental manipulation of static arm positions, he showed that when the limb is subjected to destabilizing gravitational torques, the CNS increases joint stability through cocontraction. In the present set of experiments, the magnitude of the gravitational torque at the start of movements, with and against gravity, was approximately the same. However, it is possible that when the limb moves in the same direction as the 'destabilizing' force, there is no need to increase stability at the joint. The limb moves in the direction of the gravitational force partly through generation of active force, and to some extent by succumbing to the 'destabilizing' force. Thus, the force generated by the muscle prior to movement start is relatively small and is reflected in the relatively small change in AG1 duration. In movements against gravity, the situation is more complex. Not only must the CNS generate adequate muscle activity to initiate movement, but it must also ensure that in generating large forces the limb is not subjected to unwanted perturbations (Lestienne et al. 1981). Thus, in this case, the role of the agonist is not simply to regulate acceleration but, in addition, to act with the antagonist to increase joint stiffness, creating a stable base from which to begin movement.

This study has shown that muscle activation patterns in movements performed under different gravitational loads are modified, resulting in the preservation of a common movement trajectory. What is of interest is that the CNS modulates a basic pattern of activation by taking advantage of external forces. It would appear that in planning and coordinating movement the CNS not only exploits the passive, interactive and mechanical properties of the system (Bernstein 1967) but also utilizes the various 'resources' available in the environment in which the action takes place.

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ORIGINAL PAPER

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Influence of joint interactional effects on the coordination of planar two-joint arm movements

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Abstract We have examined EMG-movement relations in two-joint planar arm movements to determine the influence of interactional torques on movement coordination. Explicitly defined combinations of elbow movements (ranging from 20 to 70°) and wrist movements (ranging from 20 to 40°) were performed during a visual, step-tracking task in which subjects were specifically required to attend to the initial and final angles at each joint. In all conditions the wrist and elbow rotated in the same direction, that is, flexion-flexion or extension-extension. Elbow movement kinematics were only slightly influenced by motion about the wrist. In contrast, the trajectory of the wrist movement was significantly influenced by uncompensated reaction torques resulting from movement about the elbow joint. At any given wrist amplitude, wrist movement duration increased and peak velocity decreased as elbow amplitude increased. In addition, as elbow amplitude increased, wrist movement onset was progressively delayed relative to this elbow movement. Surprisingly, the changes between joint movement onsets were not accompanied by corresponding changes between agonist EMG onsets at the elbow and wrist joints. The mean difference in onset times between elbow and wrist agonists (22–30 ms) remained unchanged across conditions. In addition, a basic pattern of muscle activation that scaled with movement amplitude was observed at each joint. Phasic agonist activity at the wrist and elbow joints remained remarkably similar across conditions and thus the changes in joint movement onset could not be attributed to changes in the motor commands. Rather, the calculated torques from the averaged data showed that the difference in timing of joint movement onsets was influenced by joint interactional torques. These findings suggest that during simple two-joint planar movements of the elbow and the wrist joint, the central nervous system does not alter the basic motor commands at each joint and as a result the actual trajectory of each joint is determined by interactional torques.

Key words Multijoint movement · Kinematics · EMG · Interactional torques · Human

Introduction

In searching for the strategies used by the CNS in controlling movement, the focus of study in recent years has shifted from analysis of single-joint movements to multijoint movements. It is now widely accepted that specific complexities arise during rotation about two or more joints (such as joint interactional effects resulting from reaction, centripetal, and Coriolis torques) that are not present in the single-joint case (Hollerbach and Flash 1982). In order for coordinated movement to occur, it is generally assumed that the CNS must in some manner play an active role in counteracting the effects of interactional torques and in organizing the relationship between joint movement. Thus far however, few studies have directly examined the influence of such torques during multijoint arm movements.

To date, the study of multijoint arm movements has largely been directed toward the determination of the space or "coordinate frames" in which movements are represented with an emphasis on analysis of point-to-point kinematics (Atkeson and Hollerbach 1985; Hong et al. 1994; Kaminski and Gentile 1986, 1989; Morasso 1981). Only a few studies have examined both the kinematics and the related muscle activation patterns (Accornero et al. 1984; Karst and Hasan 1991; Lacquaniti and Soechting 1982; Soechting and Lacquaniti 1981; Wadman et al. 1980). In general, multijoint movements are characterized by smooth, bell-shaped velocity profiles and are associated with a basic pattern of muscle activation, consisting of alternating EMG bursts in the agonist and antagonist muscles at each joint (Accornero et al. 1984; Karst and Hasan 1991; Wadman et al. 1980), similar to that observed in many single-joint movements

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(e.g., Brown and Cooke 1981; Cooke and Brown 1990; Hallett et al. 1975). A number of modifications have been reported in these EMG-movement relations which may be related to the forces influencing movement. For example, both the magnitude of the initial agonist EMG burst (AG1) (Wadman et al. 1980) and the time of onset of muscle activity (Flanders 1991) are dependent on movement direction. In addition initial agonist activity has been found to vary with movement direction relative to the initial orientation of the distal segment. Consequently, AG1 activity does not necessarily correlate with the direction of joint rotation (Karst and Hasan 1991). Koshland et al. (1991) have further shown that during voluntary and imposed movements of the elbow joint, muscle activity at the wrist joint acts to minimize the effect of the reaction forces at that joint resulting from elbow movement. Such activity is present regardless of whether the wrist is immobilized or is free to move, suggesting that there may be specific coupling of elbow and wrist activity under certain task conditions where voluntary movement of the wrist is not required. The question that arises is how are the EMG-movement relations modified in a two-joint task in which voluntary movement is required at both elbow and wrist joints.

We examined EMG-movement relations during a two-joint planar arm movement task where subjects were required to specifically attend to the initial and final joint angles at both the elbow and the wrist joints. The results of this study indicated that motion about the elbow was relatively unaffected by motion about the wrist. In contrast, wrist movement kinematics were directly affected by reaction torques resulting from the movement about the elbow joint. However, the muscle activation patterns at the wrist joint were not altered to counteract the effects of these reaction torques. As a result, both the actual trajectory of the wrist joint and the time of wrist movement onset were influenced by interactional torques.

Materials and methods

Experimental paradigm

Six normal subjects (aged 23–38) with no known history of motor system disorders participated in this study. Subjects performed flexion and extension movements about the elbow and wrist joints in a step-tracking paradigm. A stick-figure target composed of two connected bars, representing the forearm and hand, was displayed on a television monitor. The configuration of the two connected bars could be altered to independently set individual elbow and wrist angles. The subject's actual forearm and hand positions were displayed as two connected lines on the same monitor. The target stick-figure switched at a regular rate (every 5 s) between the initial and final elbow and wrist positions. The subject's position was refreshed every 10 ms. Subjects were required to superimpose their forearm and hand positions on the target stick-figure by moving the lines into the bar. The width of each bar corresponded to a movement amplitude of approximately 3°. Subjects were instructed to move "fast and accurately" between the target bars. Movements that were off the target amplitude by greater than 5° were discarded. This resulted in approximately 2–3% of the movements being discarded.

Subjects were seated comfortably and grasped a vertical rod attached to a biarticulated manipulandum which rotated in the horizontal plane about vertical axes at the elbow and wrist joints. Each subject's shoulder was abducted to 90° with the forearm semiprone. The forearm and the hand were supported at each pivot point. Subjects made flexion movements first followed by extension movements. The initial position for all flexion movements was 35° of elbow extension (0° equalling full extension) and 10° of wrist extension. Subjects performed all movements with their dominant arm. Three target wrist amplitudes of 20, 30 and 40° were combined with three target elbow amplitudes of 20, 40 and 70°. This resulted in a total of nine separate combinations of two-joint movement targets which were presented in a random order in a single session. In all conditions both the elbow and the wrist always rotated in the same direction, i.e. wrist flexion-elbow flexion and wrist extension-elbow extension. In each movement condition a block of 30 movements was performed consisting of 15 flexion and 15 extension movements. Presentation of each new block was preceded by a rest period of 2–3 min. Approximately 10–20 practice movements were made in each condition prior to data collection.

Data recording

The angular positions of the two joints were obtained using electrogoniometers (Penny and Giles). A crepe bandage was loosely tied around each subject's forearm. The goniometers were attached to the surface of the bandage and then secured with adhesive tape. This ensured that there was minimal artifactual movement of the goniometers. Surface EMGs were recorded from biceps, lateral head of triceps, flexor carpi radialis and extensor carpi radialis, with bipolar electrodes separated by 1 cm. All data were digitized on-line (12-bit) at 500 Hz. EMGs were filtered (10–1000 Hz) and subsequently full-wave rectified. The data were then stored for later off-line analysis.

Data analysis

Velocity and acceleration were obtained from individual flexion and extension movements by digital differentiation of the position signal. The times of the start and end of acceleration and deceleration were determined using a threshold of 130°/s². These times were used in determining movement start, movement duration, and peak velocity. Mean values for peak velocity and movement duration from each subject were used to calculate means and standard errors across all subjects. Onset times of AG1 bursts were determined using interactive graphics (Cooke and Brown 1994). Only those records in which EMG onsets could be clearly determined were used for analysis.

The moment of inertia of each subject's forearm and hand segments were calculated from Dempster's (1955) estimates. The following are the moments of inertia of the hand and forearm for one female subject: height 1.6 m, weight 61 kg; I_1 (forearm)=0.01 kg·m², I_2 (hand)=0.001 kg·m². The moments of inertia of the manipulandum were estimated to be 0.006 kg·m² for the hand segment and 0.007 kg·m² for the forearm segment. The muscle torques acting at the elbow (Tmm_1) and wrist (Tmm_2) joints were calculated using the following equations (Hollerbach and Flash 1982; Karst and Hasan 1991):

$$
\begin{aligned}
Tmm_1 = {} & [I_1 + I_2 + m_1c_1^2 + m_2(l_1^2 + c_2^2 + 2l_1c_2\cos\theta_1)]\,\alpha_1 \\
& + (I_2 + m_2c_2^2 + m_2l_1c_2\cos\theta_2)\,\alpha_2 - (m_2l_1c_2\sin\theta_2)\,\omega_2^2 \\
& - (2m_2l_1c_2\sin\theta_2)\,\omega_1\omega_2
\end{aligned}
$$

$$
Tmm_2 = (I_2 + m_2c_2^2 + m_2l_1c_2\cos\theta_2)\,\alpha_1 + (I_2 + m_2c_2^2)\alpha_2 + (m_2l_1c_2\sin\theta_2)\,\omega_1^2
$$

where θ_1,θ_2 are joint angles, ω_1,ω_2 are angular velocities, α_1,α_2 are angular accelerations; I_1 and I_2 are the moments of inertia of the forearm and hand, respectively, about the center of mass, m_1, m_2 are the segment masses, l_1 and l_2 are the segment lengths, c_1 and c_2 are distance from the center of mass to the proximal end of segment. The terms with angular velocity squared are the centripe-

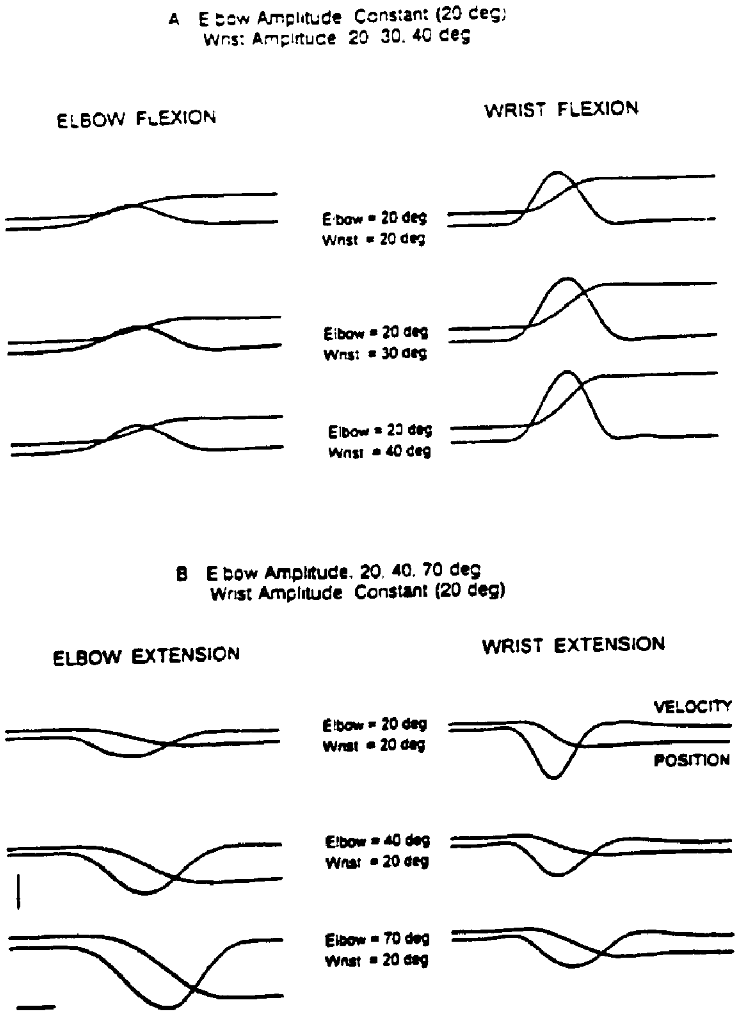

Fig 1A,B Two-joint elbow and wrist movements in the same direction Records of position and velocity from combined flexion-flexion elbow and wrist movements (A) and combined extension-extension elbow and wrist movements (B) are shown Each record is the mean of 15 movements Records were aligned to movement start for averaging Vertical position and velocity calibration represent 30° and 130°/s, respectively Horizontal calibration represents 100 ms

tal torques. For each joint the terms with the angular accelerations of the other joint are the reaction torques and the terms with the angular accelerations of the same joint are the net torques. For the wrist joint the equation can be written as.

$$T_{mus}=T_{reaction}+T_{net}+T_{centripetal}$$

Results

Movement kinematics

A sample of some of the different two-joint movement conditions used in this experiment are illustrated in Fig. 1. Averaged position and velocity records of elbow and wrist movements from one representative subject are shown. In Fig. 1A, wrist flexion movements of three different amplitudes (20, 30, and 40°) combined with elbow flexion of 20° are shown. Figure 1B illustrates elbow extension movements of three different amplitudes (20, 40, and 70°) from the same subject, combined with wrist extension of 20°. In all conditions the wrist and elbow rotated in the same direction, that is, flexion-flexion or extension-extension. Subjects performed both flexion and extension movements under all conditions. Note that the characteristic bell-shaped velocity profile was observed at the two joints in all conditions.

A qualitative examination of Fig. 1 shows that the kinematics of the wrist movements were influenced by concurrent elbow movements. In contrast, the same figure shows that the kinematics of the elbow movement were little affected. This was confirmed by plotting kinematic parameters of movements about one joint as a function of movement amplitude of the other joint. The relations of movement duration and peak velocity with movement amplitude across six subjects are shown in Fig. 2. Figure 2A and B show data from elbow extension movements plotted as a function of *wrist* amplitude. Figure 2A shows that there was very little change in the el-

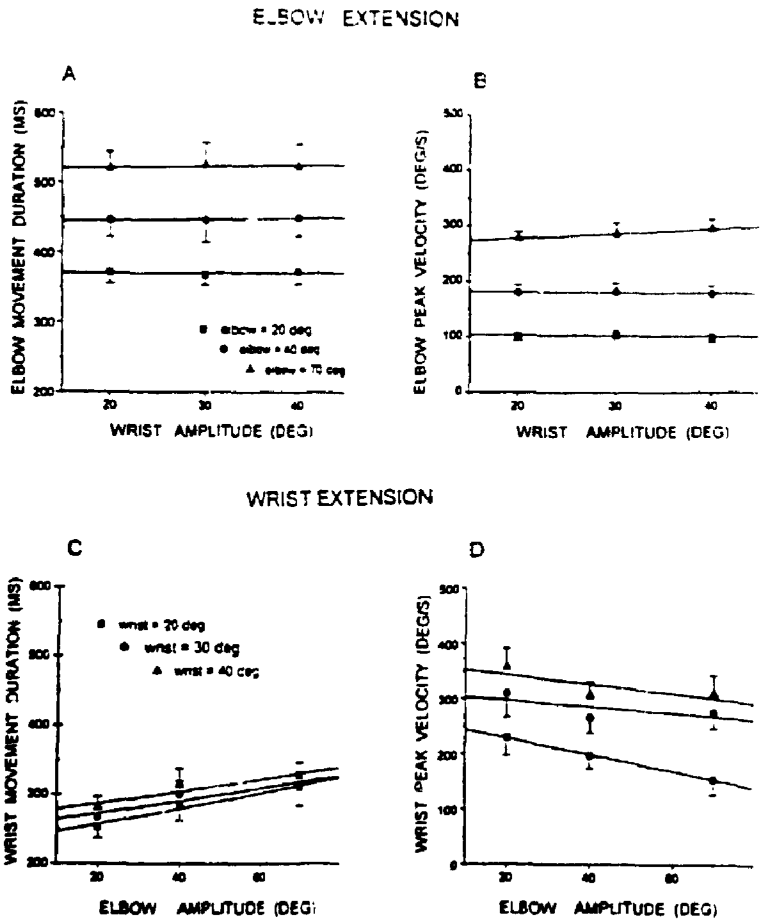

Fig 2A–D Kinematic relations of one joint plotted as a function of the second joint A Elbow movement duration B elbow peak velocity C wrist movement duration and D wrist peak velocity Each point is the mean obtained from six subjects *Error bars* are 1 SEM *Solid lines* are the best-fit linear regression lines

bow movement duration with wrist amplitude (Fig. 2A), as indicated by the slopes of the best-fit linear regression lines (slopes ranged from 0.1 to 0.2 ms/deg). No significant differences were found between the slopes for different elbow amplitudes ($P>0.6$). At each wrist amplitude, elbow movement duration increased significantly as elbow amplitude increased ($P<0.03$). Figure 2B illustrates that there was a small change in elbow peak velocity with wrist amplitude (slopes of the regression lines ranged from −0.2 to 0.8°/s per degree). At all wrist amplitudes, elbow peak velocity increased significantly as elbow amplitude increased ($P<0.0003$). Although not shown, similar relationships were observed for elbow flexion movements. Thus, elbow kinematics were not significantly influenced by motion of the wrist.

Figure 2C shows wrist extension movement duration plotted as a function of *elbow* amplitude. A large increase was observed in wrist movement duration as elbow amplitude increased (slopes of the linear regression lines ranged from 0.9 to 1.1 ms/deg). There were no significant differences between the slopes at the different wrist amplitudes ($P>0.7$) It should be noted that there were no significant differences in wrist movement durations as wrist movement amplitude increased at any given elbow amplitude ($P>0.1$). This is in contrast to the increase normally observed in movements about a single joint (Benecke et al. 1985; Brown and Cooke 1984). Figure 2D shows that at all wrist amplitudes, wrist peak velocity decreased with elbow amplitude (slopes ranged from −0.6 to −1.5°/s per degree). There were no significant difference in the slopes ($P>0.2$). At each elbow amplitude, wrist peak velocity increased significantly with wrist amplitude ($P<0.01$). Similar relationships were observed for wrist flexion movements. In contrast to elbow movements, both wrist movement duration and peak velocity were highly dependent on the amplitude of concurrent elbow movement.

Muscle activation patterns

In many single joint movements both the magnitude and the duration of the initial agonist burst (AG1) increase

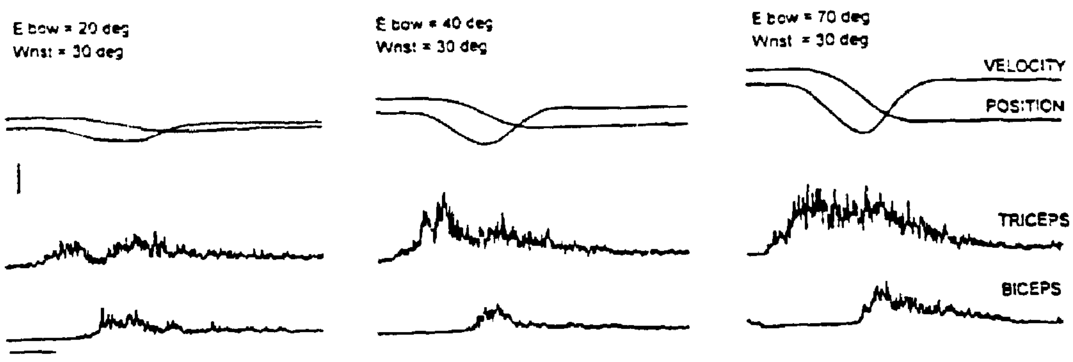

Fig. 3 Qualitative changes in elbow EMG activity as a function of amplitude In each set of records are shown averaged position velocity, and EMG activity for elbow extension movements of three amplitudes (20, 40, and 70°) that were combined with 30° wrist extension movements Traces are the mean of 15 movements Records were aligned to elbow movement start for averaging Vertical position and velocity calibration represent 40° and 230°/s, respectively Horizontal calibration represents 100 ms

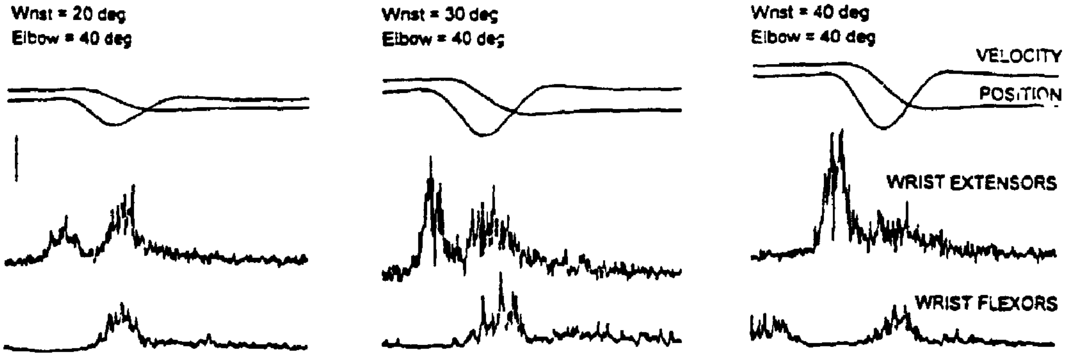

Fig. 4 Qualitative changes in wrist EMG activity as a function of amplitude In each set of records are shown averaged position, velocity, and EMG activity for wrist extension movements of three amplitudes (20, 30, and 40°) that were combined with 40° elbow extension movements. Traces are the mean of 15 movements Records were aligned to wrist movement start for averaging Vertical position and calibration represent 40° and 320°/s, respectively Horizontal calibration represents 100 ms

with movement amplitude (Brown and Cooke 1984; Hallett and Marsden 1979). In the present two-joint task, the changes in AG1 magnitude with movement amplitude at both the elbow and the wrist joints were qualitatively similar to those observed in movements about a single joint. For example, Fig. 3 shows that phasic activity in the elbow agonist generally increased as amplitude increased during extension-extension movements. Similarly, in Fig. 4 phasic activity in the wrist agonist increased as wrist amplitude increased from 20 to 40° during extension-extension movements.

Given that there were no significant changes in the elbow movement kinematics at any given amplitude as a function of wrist amplitude, we examined the underlying EMGs in more detail to determine the strategy used by the central nervous system (CNS) to produce such consistent trajectories. Figure 5 shows movement kinematics and associated EMGs for constant-amplitude (40°) elbow flexion movements made in conjunction with three different amplitudes of wrist movement. As seen previously, there was little change in elbow kinematics as the wrist movement amplitude increased. In addition, it appeared that phasic EMG activity related to elbow movement changed little across all conditions. This implies that reaction torques resulting from motion about the wrist produced little, if any, effect on motion of the elbow and thus no significant compensation was required in terms of muscle activity to preserve a common trajectory.

In contrast, Fig. 6 shows that elbow movement clearly affected wrist movement. Constant-amplitude wrist extension movements made in conjunction with elbow movements of three different amplitudes are shown. As described previously, wrist movement duration increased and peak velocity decreased as elbow amplitude increased. Interestingly, however, these changes in movement kinematics were not accompanied by corresponding changes in the muscle activation patterns. In fact, the phasic agonist activity at the wrist remained remarkably similar as elbow amplitude increased.

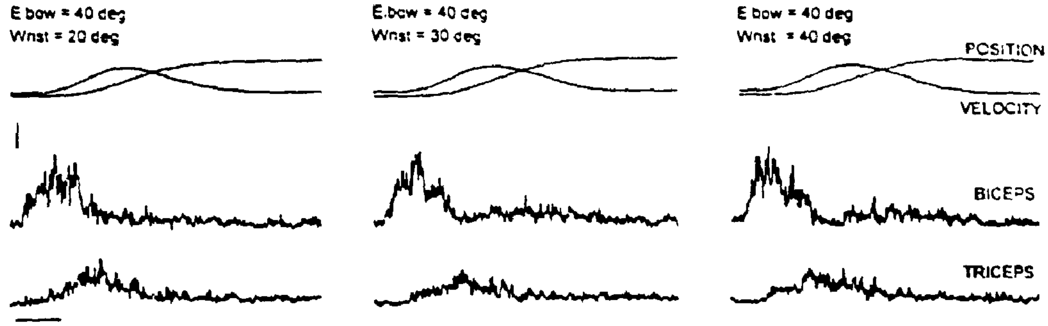

Fig. 5 Elbow EMG activity as a function of wrist amplitude. Averaged position, velocity, and EMG activity for elbow flexion movements of 40° are shown. These movements were combined with wrist flexion movements of 20, 30, and 40°. Records are the mean of 15 movements. Records were aligned to elbow movement start for averaging. Vertical position and velocity calibration represents 40° and 140°/s. Horizontal calibration represents 100 ms

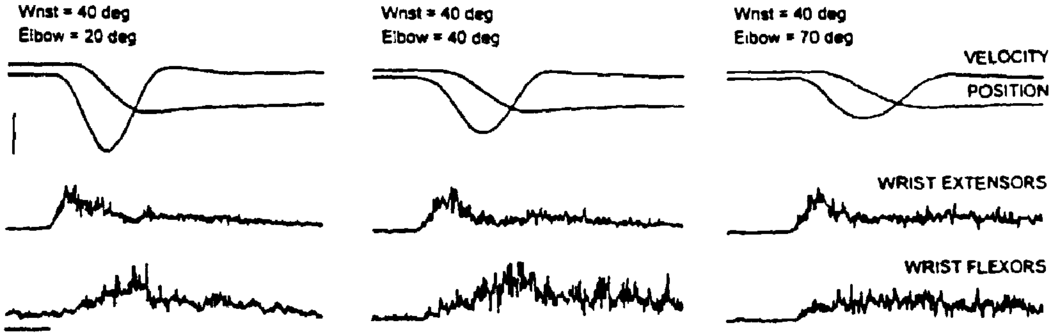

Fig. 6 Wrist EMG activity as a function of elbow amplitude. Averaged position, velocity, and EMG activity for wrist extension movements of 40° are shown. These movements were combined with elbow flexion movements of 20, 40, and 70°. Records are the mean of 15 movements. Records were aligned to wrist movement start for averaging. Vertical position and velocity calibration represent 40° and 220°/s. Horizontal calibration represents 100 ms

Movement onset

In addition to changes in wrist kinematics, differences were observed in the time of movement onset between the elbow and wrist joints. The graph on the left of Fig. 7 shows the mean time difference between elbow and wrist movement onsets as a function of wrist amplitude for all six subjects. Positive values indicate that elbow movement started before the wrist movement. In all conditions, elbow movement onset preceded wrist movement onset and this difference increased as elbow movement amplitude increased ($P<0.08$). For example, for 20° wrist movements, the mean movement onset difference increased from 16 (±12) to 50 (± 20) ms as elbow amplitude increased from 20 to 70°.

This difference in joint movement onsets with changes in elbow amplitude was not accompanied by a similar change in the onsets of the EMG bursts occurring in elbow and wrist agonists. The right-hand graph of Fig. 7 shows the time difference between AG1 onsets from three subjects (in whom AG1 onsets could be clearly determined). The mean onset difference ranged from 22 (±15) to 30 (±19) ms. These values are comparable with those reported by Karst and Hasan (1991) and Wadman et al. (1980) for movements about the shoulder and elbow joints. As elbow amplitude increased, the difference in AG1 onsets remained unchanged at both 30° and 40° wrist amplitudes ($P>0.8$). Thus while the relative timings of movement onsets changed, this was not associated with changes in the onsets of the AG1 bursts, which is normally thought to initiate movements.

Torque profiles

The observation that phasic EMG activity at the wrist changed little while movement kinematics changed suggested that interactional torques arising from elbow movement may have affected the wrist trajectories. In order to determine the influence of elbow movement on wrist movement, the torques acting at the wrist joint were calculated from averaged velocity and acceleration records. Figure 8 shows the calculated torques from the averaged data of one representative subject for a constant

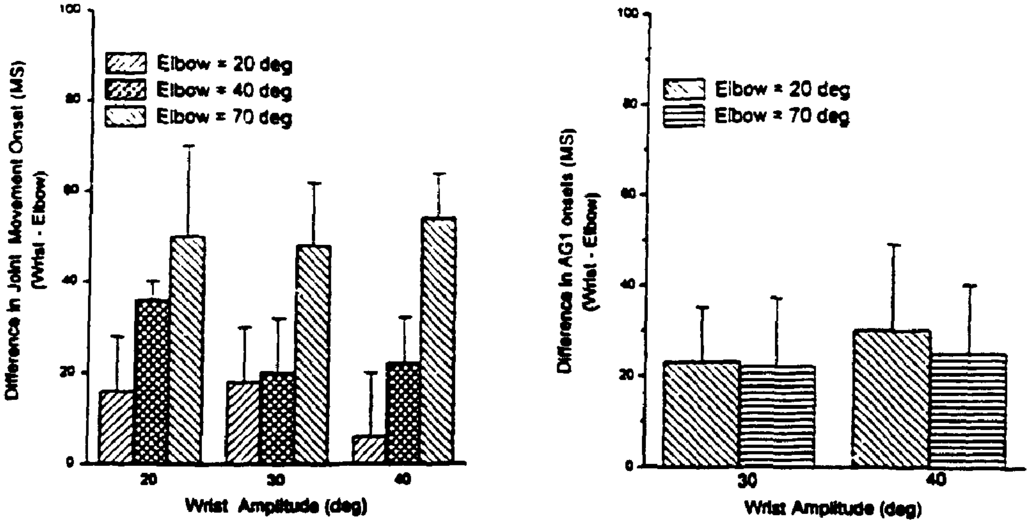

Fig. 7 Differences in movement onset and initial agonist EMG burst (AG1) onset between the elbow and wrist joints. *Left*, mean time difference between elbow flexion and wrist flexion movement onset as a function of wrist amplitude. Each *bar* represents data from six subjects. *Right*, mean time difference between onset of phasic agonist activity at the elbow and wrist joints Each *bar* represents data from three subjects. *Error bars* are 1 SEM

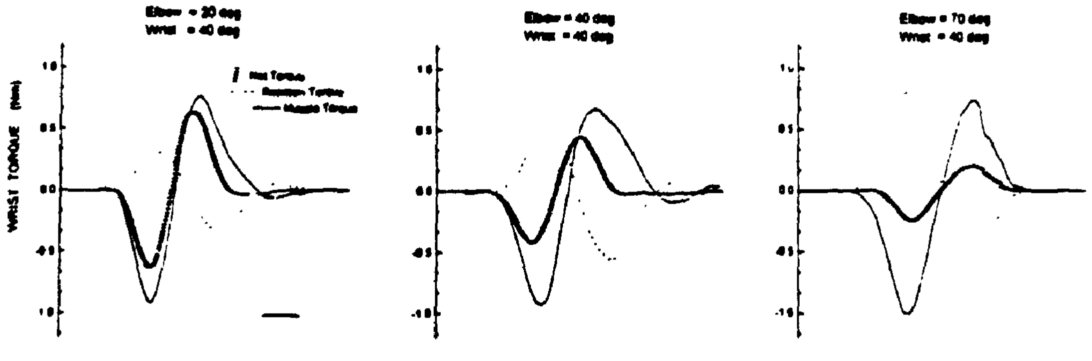

Fig. 8 Calculated torques acting at the wrist joint. Records of the reaction, muscle and net torque acting at the wrist during wrist extension movements of 40° are shown. These movements were combined with elbow extension movements of 20, 40, and 70° Traces are the mean of 15 movements. Records were aligned to elbow movement start for averaging

wrist movement amplitude of 40° combined with increasing elbow movement amplitudes. As elbow movement amplitude increased (from 20 to 70°), the peak reaction torque at the wrist increased from about 0.3 to 0.8 Nm. In contrast, the amplitude of the peak muscle torque only increased from about 0.8 Nm to 1.0 Nm. Since the reaction torque (which opposed the movement) increased, and there was no corresponding increase in the muscle torque, the net torque driving the wrist decreased. Consequently, larger elbow movements were associated with smaller wrist accelerations.

It is of particular interest to note in this figure that onset of the net wrist torque (and therefore wrist acceleration onset) gradually shifts at larger elbow amplitudes. As shown previously, changes in joint onset times did not result from a change in EMG onsets. Examination of the torques indicated that this shift was due to the interaction of elbow reaction torques and wrist muscle torques. At 20° elbow amplitude, the magnitude of the wrist muscle torque was larger than the magnitude of the elbow reaction torque at movement start and wrist acceleration began at about the same time as elbow acceleration. However, for the 70° elbow movement the magnitudes of the wrist muscle torque and elbow reaction torques were approximately equal at the start of movement. Thus, the time at which the muscle torque exceeded the elbow reaction torque was delayed and consequently the onset of wrist acceleration was delayed.

Discussion

One of the primary unresolved issues in multijoint movement control is the identification of the coordinates in which movements are represented. In attempting to resolve this issue most investigators have focused their analysis either on movement kinematics of the hand or the kinematic relationship between joints. Many early studies reported straight line hand paths and bell-shaped hand velocity profiles during movement, providing evidence for endpoint control (Morasso 1981, Abend et al 1982). The implication underlying this strategy is that hand trajectories would be transformed into joint rotations and the required joint torques derived by inverse kinematic transformations (Hollerbach 1990) More recently, Atkeson and Hollerbach (1985) proposed a planning strategy based on staggered joint interpolation, i.e., the time at which joints start or stop moving may be staggered with respect to each other, with a common movement profile observed at all joints. This strategy was thought to be more advantageous in that it required less complex, direct kinematic transformations (Hollerbach 1990). Although there has been some experimental evidence to support this hypothesis (Kaminski and Gentile 1986, 1989), the mechanisms by which joint movement onsets may be regulated remain very unclear.

One obvious assumption is that, if the CNS was in some manner actively shifting joint onset times, this would be reflected in the onset times of agonist muscle activity. However, our observations do not support this assumption. The results of the present study show that timing differences between the onset times of elbow and wrist movements were not accompanied by corresponding changes in the onsets of elbow and wrist EMG. This finding is similar to that reported by Karst and Hasan (1991), who showed that no significant correlation existed between the difference in agonist onsets and joint movement onsets for two-joint shoulder and elbow movements. It should be further noted that the relative timings of agonist onsets remained unchanged across the various movement conditions used in this experiment. Although the possibility that changes in AG1 onset may have occurred in other muscles that were not recorded in this study must be considered, our analysis suggests that the observed changes in joint movement onsets could be explained simply on the basis of joint interactional effects.

As mentioned previously, the actual trajectory of the wrist movement was influenced both by the wrist muscle torques and the reaction torques arising from movement about the elbow. The interaction between these torques also affected the timing of wrist movement onset. In conditions where the elbow amplitude was quite small, the magnitude of the wrist muscle torque was larger than the magnitude of the elbow reaction torque and thus wrist movement started at about the same time, or followed shortly after elbow movement onset. At larger elbow amplitudes (i.e., 70°), the wrist muscle torque and reaction torque acting at the wrist were equal and opposite in magnitude at the start of movement As a result wrist movement onset occurred much later at a point where muscle torque started to exceed the reaction torque Thus the relative timing of joint movement onsets was influenced by interactional torques and not directly determined by the CNS

In terms of agonist onset timing there are two factors that must be considered in multijoint movement planning. One is the determination of which joint to activate first. This decision may be made on the basis of the relative inertia of individual segments or possibly the relative amplitudes of the movements about the two joints Once movement about the first joint has been initiated, the onset of movement at the second joint may be determined on the basis of movement direction (Karst and Hasan 1991; Wadman et al. 1980), or more simply on the direction of desired joint rotation (taking into account the muscle and interactional torques) The location of the target may then determine the selection of the initial muscle activity (Koshland and Hasan 1994)

Once the timing has been resolved, how does the CNS select a particular level of activity (for any particular joint) that is sufficient to produce movements of the same amplitude, regardless of movements about the second joint? It is quite possible that this selection is based on EMG-movement relationships derived from the single-joint case. Hong et al (1994) have recently shown that the relationship between the EMG muscle activation patterns and torque during a two-joint movement involving the shoulder and elbow is similar to that observed in movements about a single joint In the present task, for example, larger movement amplitudes were associated, qualitatively, with increases in AG1 magnitude at both elbow and wrist joints, and basic patterns of muscle activation were observed that were similar to those observed in single-joint movements. The difference in these movements was that, in the case of wrist movements, qualitatively similar patterns of muscle activity could be associated with movements of different movement durations and magnitudes of peak velocity, though the overall time symmetric structure of the movement remained the same. Our analysis revealed, however, that these observed kinematic differences could be directly attributed to joint interactional effects. It is interesting to note that the CNS did not counteract elbow reaction torques in order to maintain an identical trajectory for wrist movements of the same amplitude, particularly since this has been observed in single-joint movements (Virji-Babul et al. 1994). Rather, a common pattern of muscle activity was employed for all wrist movements of the same amplitude, regardless of elbow amplitude. The use of a common pattern of muscle activation based on EMG-movement relations in single-joint movements may therefore be a strategy to simplify the coordination of two-joint movements.

It should be pointed out that our present results may be directly influenced by the constraints imposed by the task itself. Although no specific requirements were made with regard to the speed or accuracy, the paradigm used in this study did force subjects to focus on individual joint angles rather than the endpoint target. However, the consistency of our results with those of other studies that used endpoint targets (Karst and Hasan 1991, Wadman et al. 1980) suggests that planning strategies may not be directly influenced by the nature of the external target. It is quite possible that, as tasks become more complex, the external requirements may influence planning strategies to a greater extent. Nonetheless, our results would indicate that, in moving from single-joint movements to movements about two joints where the task requirements are relatively simple, the CNS is less concerned about maintaining specific movement characteristics. We suggest therefore that the CNS plans movements only very globally at the joint level, and that the actual trajectory of the movement is not planned but emerges as a result of the integration of basic patterns of muscle activity with dynamic interactions between joints.

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RESEARCH ARTICLE

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Reprogramming of muscle activation patterns at the wrist in compensation for elbow reaction torques during planar two-joint arm movements

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Abstract The relationship between wrist kinematics, dynamics and the pattern of muscle activation were examined during a two-joint planar movement in which the two joints moved in opposite directions, i.e. elbow flexion/wrist extension and elbow extension/wrist flexion. Elbow movements (ranging from 10 to 70 deg) and wrist movements (ranging from 10 to 50 deg) were performed during a visual, step-tracking task in which subjects were required to attend to the initial and final angles at each joint. As the elbow amplitude increased, wrist movement duration increased and the wrist movement trajectories became quite variable. Analysis of the torques acting at the wrist joint showed that elbow movements produced reaction torques acting in the same direction as the intended wrist movement. Distinct patterns of muscle activation were observed at the wrist joint that were dependent on the relative magnitude of the elbow reaction torque in relation to the net wrist torque. When the magnitude of the elbow reaction torque was quite small, the wrist agonist was activated first. As the magnitude of the elbow reaction torque increased, activity in the wrist agonist decreased significantly. In conditions where the elbow reaction torque was much larger than the net wrist torque, the wrist muscle torque reversed direction to oppose the intended movement. This reversal of wrist muscle torque was directly associated with a change in the pattern of muscle activation where the wrist antagonist was activated prior to the wrist agonist. Our findings indicate that motion of the elbow joint is an important consideration in planning wrist movement. Specifically, the selection of muscle activation patterns at the wrist is dependent on the relative magnitude and direction of the elbow reaction torque in relation to the direction of wrist motion.

Key words Multi-joint movement · Dynamics
Kinematics · EMG · Human

Introduction

In attempting to understand the control of arm movements, the focus of study has recently shifted from single- to multi-joint movements. It is now well established that, during multi-joint movements, motion at each joint is influenced by both muscle torques as well as by dynamic interactional torques from other moving segments. Although there are commonalities in the EMG-movement relations between single- and multi-joint movements (Hong et al. 1994; Karst and Hasan 1991; Virji-Babul and Cooke 1995; Wadman et al. 1980), the specific variables used in planning multi-joint movements have yet to be clearly identified. In particular, the rules used by the nervous system in selecting the appropriate muscle activation patterns to achieve coordination between joints remain equivocal.

Koshland and Hasan (1994) have proposed that target location may be one important planning variable during multi-joint movements. They observed that the selection of initial muscle activity was correlated with target location and that altering the relative joint amplitudes did not affect this activity. For their studies, they specifically utilised three joint movements where the degrees of freedom permit more than one solution of an end-point positioning task in terms of specific joint angles. We have found recently that, during two-joint movements in which the required joint angles were explicitly specified, the overall muscle activation pattern at each joint remained the same despite changes in target location. For the wrist joint, selection of muscle activity appeared to be dependent on the amplitude of wrist movement and was not altered by changing

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the excursion of the elbow joint (Virji-Babul and Cooke 1995). Furthermore, the movement trajectory at the wrist was significantly influenced by reaction torques resulting from elbow movement.

In order to further examine the variables involved in planning movement, we studied wrist movement during a two-joint planar movement task, involving the elbow and wrist joints, in which the two joints moved in opposite directions. We were particularly interested in analysing the relationship between the wrist kinematics, dynamics and muscle activation patterns, since in this configuration the reaction torques at the wrist resulting from elbow movement act in the same direction as the intended wrist movement and would, therefore, assist wrist movement. Since increases in elbow acceleration would result in larger reaction torques at the wrist, we asked how muscle activation patterns at the wrist joint are modified in order to account for such increases. Our findings indicate that muscle activity at the wrist is preselected on the basis of the magnitude and direction of the reaction torques that would be produced by movement about the elbow joint.

Materials and methods

Experimental paradigm

Five normal subjects (aged 24–55 years) with no known history of motor system disorders participated in this study. Subjects performed flexion and extension movements about the elbow and wrist joints in a step-tracking paradigm. A stick figure target composed of two connected bars, representing the forearm and hand, was displayed on a computer monitor. The configuration of the two connected lines could be altered to independently set individual desired elbow and wrist angles. The subject's actual forearm and hand positions were displayed as two connected lines on the same monitor (see Fig. 1). The target stick figure switched at a regular rate (every 5 s) between the desired combinations of elbow and wrist positions. The display of the subject's forearm and hand position was refreshed every 10 ms. Subjects were required to superimpose their forearm and hand positions on the target stick figure by moving the lines into the bar. The width of each bar corresponded to a movement amplitude of approximately 3 deg. Subjects were instructed to move "fast and accurately" between the target bars. Movements that were off the target position by more than 5 deg were discarded. This resulted in approximately 5% of the movements being discarded.

Subjects were seated comfortably and grasped a vertical rod attached to a biarticulated manipulandum which rotated in the horizontal plane about vertical axes at the elbow and wrist joints. Each subject's shoulder was adducted to 90 deg, with the forearm semiprone. The forearm and hand were supported at each pivot point. The initial position of the forearm in all conditions was 35 deg of elbow extension (0 deg equalling full elbow extension). The starting position of the hand segment was in 10 deg of wrist flexion. Subjects performed all movements with their dominant arm.

Subjects made a combined elbow flexion/wrist extension movement followed by an elbow extension/wrist flexion movement. This sequence was then repeated. Target wrist amplitudes of 10, 30 and 50 deg were combined with target elbow amplitudes of 10, 40 and 70 deg. This resulted in a total of nine separate combinations of two-joint movement targets, which were presented in a random order, in a single session. In each movement condition, a block of 30 movements was performed consisting of 15 elbow flexion/wrist extension movements and 15 elbow extension/wrist flexion movements. Presentation of each new block was preceded by a rest period of 2–3 min. Due to the novelty of the task condition, subjects made approximately 100 practice movements at the start of the experiment to learn the required movement.

Data recording

The angular positions of the two joints were obtained from precision potentiometers. Surface EMGs were recorded from biceps, lateral head of triceps, flexor carpi radialis and extensor carpi radialis with bipolar electrodes separated by 1 cm. All data were digitized online (12 bit) at 500 Hz. EMGs were filtered (10–1000 Hz) and digitized online at 500 Hz and subsequently full-wave rectified. The data were then stored for later off-line analysis.

Data analysis

The times of the start and end of movement were determined from individual movements by digital differentiation of the position signal using a threshold of 8 deg/s. These times were then used in determining movement duration. Mean values for movement start and movement duration from each subject were used to calculate means and standard errors across all subjects.

The moment of inertia of each subject's forearm and hand segments were calculated from Dempster's (1955) estimates. The muscle torques acting at the elbow and wrist were calculated using the equations of motion described by Hollerbach and Flash (1982) and Karst and Hasan (1991). (For further details, see Virji-Babul and Cooke 1995). As in our previous paper, we will use the following nomenclature. *Reaction torque* refers to the torque arising at one joint as a result of or in reaction to motion about another joint. *Net torque* refers to the summed or total of all torques acting at a joint. *Muscle torque* refers to those torques generated at a joint by the active contraction of muscles acting around the joint. Muscle torque is calculated here as the difference between net and reaction torques.

Results

Movement kinematics

A sample of some of the different two-joint movement conditions used in this experiment are illustrated in Fig. 1. Averaged position and velocity records of elbow and wrist movements from one representative subject are shown. In all conditions, the wrist and elbow rotated in opposite directions, i.e. flexion/extension or extension/flexion. In Fig. 1A, wrist extension movements of three different amplitudes (10, 30 and 50 deg) combined with elbow flexions of 40 deg are shown. Note that wrist movement duration and peak velocity increased as wrist amplitude increased. There was little qualitative change in the shape of the elbow velocity profile as wrist amplitude increased. Figure 1B illustrates wrist extension movements of 50 deg combined with elbow flexion movements of three different amplitudes (10, 40 and 70 deg) from the same subject. As expected, elbow movement duration and peak velocity increased with elbow amplitude. In contrast to the consistent elbow profiles observed in Fig. 1A, there were quite striking changes in the shape of the wrist

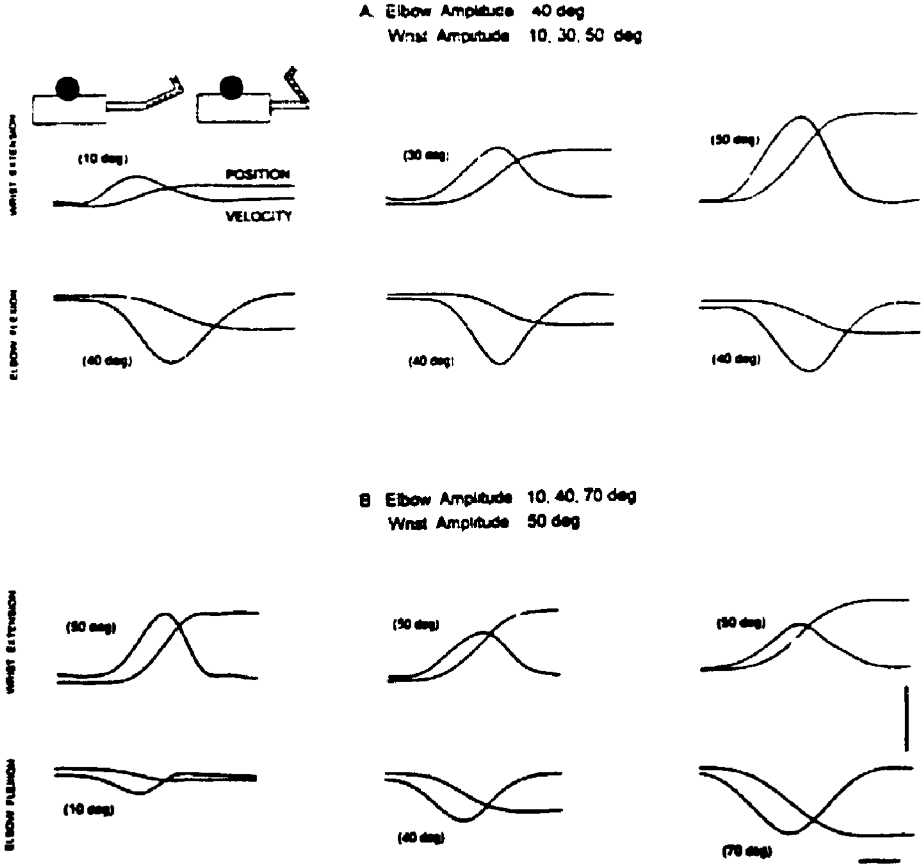

Fig. 1A, B Two-joint elbow and wrist movements in opposite directions. Records of position and velocity from combined elbow flexion/wrist extension movements are shown. **A** Wrist extension movements of three amplitudes (10, 30 and 50 deg) combined with 40-deg elbow flexion movements. **B** Elbow flexion movements of three amplitudes (10, 40 and 70 deg) combined with 50-deg wrist extension movements. Traces are the average of 15 movements. Records were aligned to movement start for averaging. Vertical velocity calibration represents 200 deg/s (A) and 400 deg/s (B). Horizontal calibration represents 100 ms

velocity profile as elbow amplitude increased. In general, wrist movement duration increased and peak velocity decreased.

Quantitatively, wrist kinematics were also affected to a greater extent by concurrent elbow movements than the reverse. Figure 2 shows the duration of movements at one joint plotted as a function of movement amplitude at the other joint. In Fig. 2A, elbow movement duration is plotted as a function of wrist amplitude. There was little change in elbow movement duration with wrist amplitude as indicated by the slopes of the best fit linear regression lines (slopes ranged from –0.7 to 0.7 ms/deg). Note that at any given wrist amplitude, elbow movement duration increased as elbow amplitude increased. Figure 2B shows the changes in the duration of wrist movement as a function of elbow amplitude. In contrast to elbow movements, wrist movement duration tended to increase as elbow amplitude increased (slopes of the linear regression lines ranged from 0.6 ms/deg for 10-deg wrist movements to 3 ms/deg for 50-deg wrist movements). Similar relationships were observed for the combination of elbow extension/wrist flexion movements. Wrist movement duration, particularly at the larger amplitudes, appeared to more affected by the amplitude of concurrent elbow movement than was elbow movement duration by the amplitude of the wrist movement.

Torque profiles

We have previously shown that during two-joint wrist and elbow movements in the same direction, changes in wrist kinematics were directly related to joint interactional effects (Virji-Babul and Cooke 1995). The changes in wrist kinematics as a function of elbow movement amplitude in the present experiment suggested that interactional torques arising from elbow

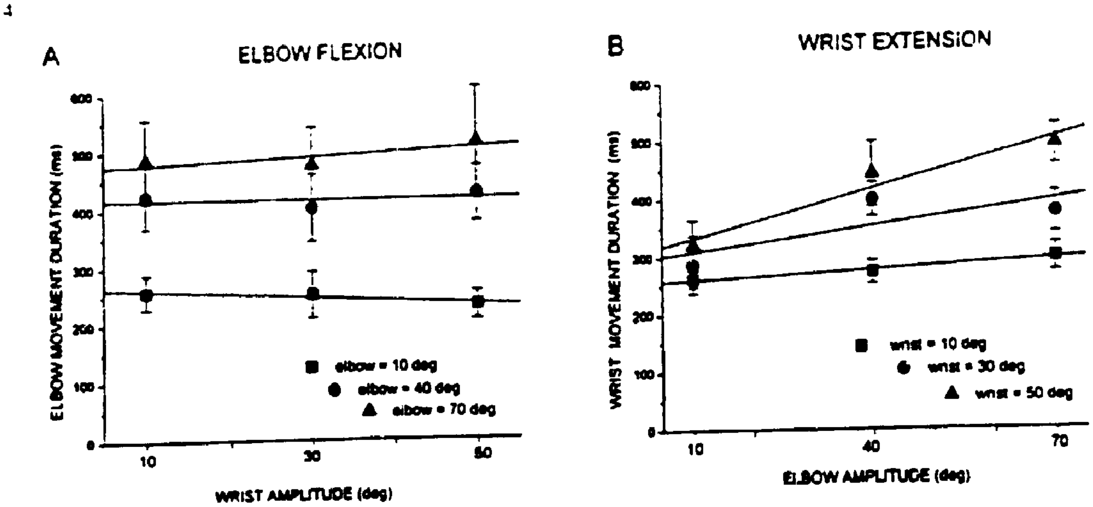

Fig. 2A, B Movement duration-amplitude relations. Elbow flexion movement duration is plotted as a function of wrist amplitude (A), and wrist extension movement duration is plotted as a function of elbow amplitude (B) Each point is the average obtained from five subjects *Error bars* are 1 SEM *Solid lines* are the best-fit linear regression lines

movement were, in some manner, influencing the wrist trajectory. In order to determine the nature of this influence, the torques acting at the wrist joint were calculated from averaged velocity and acceleration records (see Virji-Babul and Cooke 1995 for details of calculations). Figure 3 shows the calculated torques acting at the wrist from the averaged data of one representative subject. Torques are shown for wrist extensions of 10 deg combined with increasing elbow flexion amplitudes (upper panel) and of wrist flexions of 50 deg combined with increasing elbow extension amplitudes

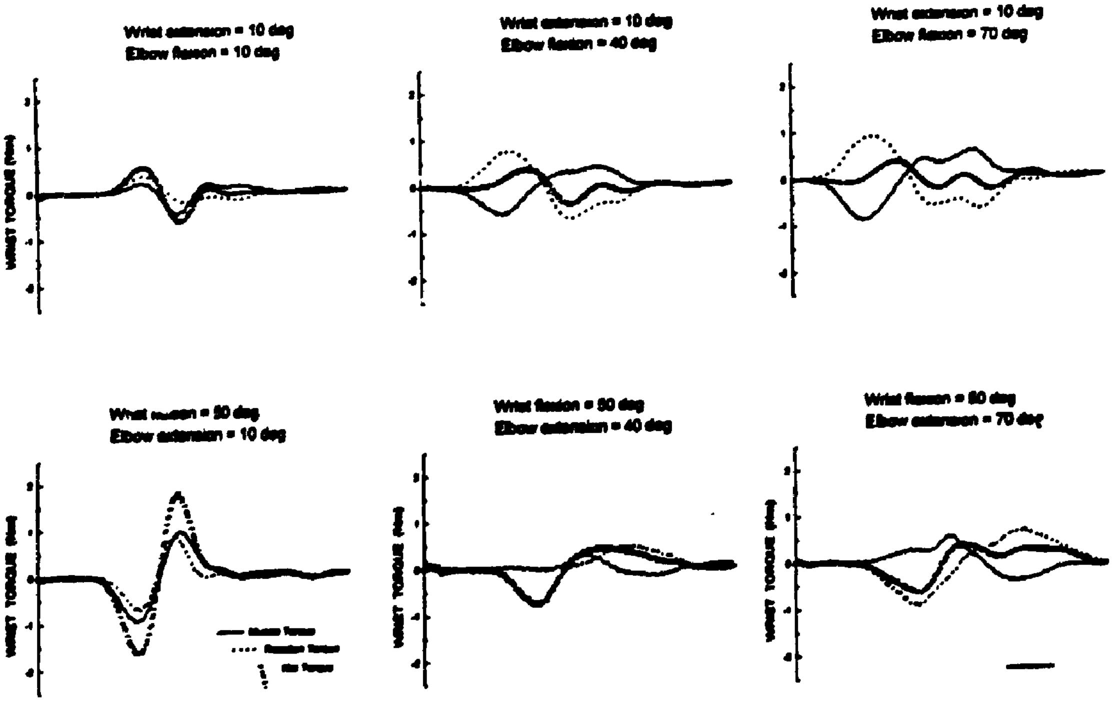

Fig. 3 Calculated torques acting at the wrist joint Records of the reaction, muscle and net torques acting at the wrist during wrist extension movements of 10 deg combined with elbow flexion movements of 10, 40 and 70 deg (*top*) and wrist flexion movements of 50 deg combined with elbow extension movements of 10, 40 and 70 deg (*bottom*) Traces are the average of 15 movements

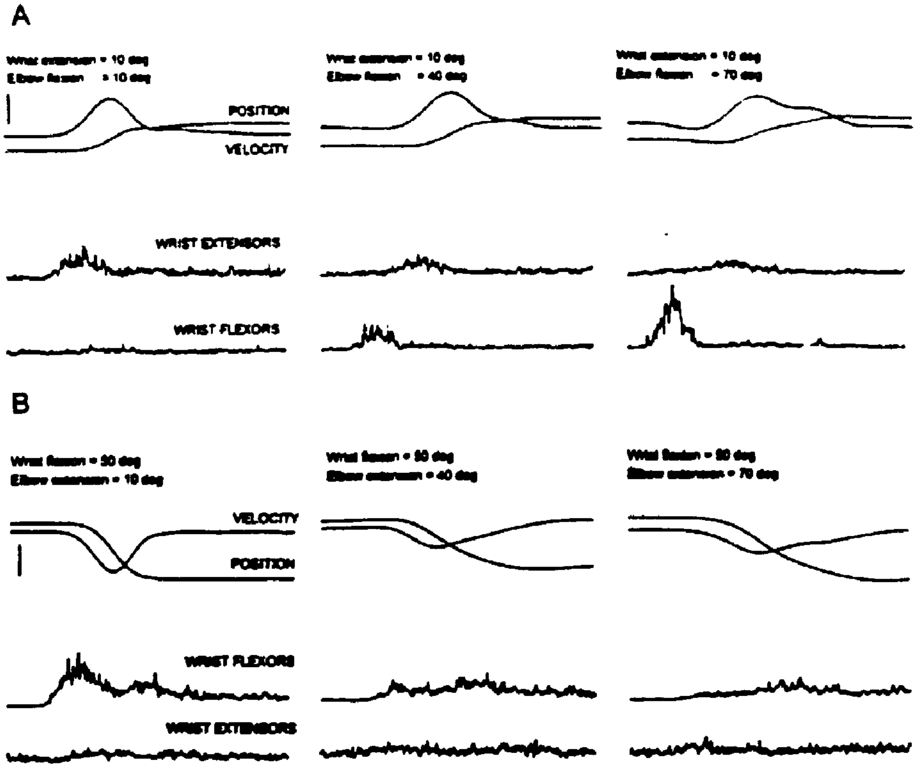

Fig. 4A, B Wrist EMG activity as a function of elbow amplitude. In each set of records are shown averaged position, velocity and EMG activity for wrist extension movements. (A) Wrist extension movements of 10 deg combined with elbow flexion movements of 10, 40 and 70 deg. **B** Wrist flexion movements of 50 deg combined with elbow extension movements of 10, 40 and 70 deg. Records are the average of 15 movements. Records were aligned to wrist movement start for averaging. Vertical velocity calibration represents 200 deg/s (A) and 400 deg/s (B). Horizontal calibration represents 100 ms

(lower panel). In all conditions, the reaction torque at the wrist resulting from elbow movement acted in the same direction as the net wrist torque. Thus, movement about the elbow produced a torque that assisted the intended wrist movement. As elbow amplitude increased (from 10 to 70 deg) and the magnitude of elbow acceleration increased, the peak reaction torque at the wrist increased and indeed, exceeded the maximum net torque acting at the wrist. This was particularly evident in large elbow movements combined with small wrist movements (Fig. 3, upper panel). Under such conditions the wrist muscle torque reversed direction and *opposed* the intended movement. Consequently, the net torque driving the wrist movement decreased and larger elbow movements were associated with smaller wrist accelerations. In contrast, the magnitudes of the peak elbow reaction torque and the net wrist torque were approximately equal in conditions where large-amplitude elbow movements were combined with large-amplitude wrist movements. Thus, as elbow amplitude increased, the desired movement was produced by decreasing the magnitude of the wrist muscle torque rather than reversing its direction.

Muscle activation patterns

The changes in the calculated wrist muscle torques suggested that the muscle activation patterns at the wrist were being modified in relation to the reaction torques acting at the wrist as a result of elbow acceleration. In Fig. 4, typical EMG activity from wrist extension movements of 10 deg and wrist flexion movements of 50 deg made in conjunction with elbow movements of three different amplitudes are shown. As described previously, wrist movement duration increased as elbow amplitude increased. In addition, note that the wrist velocity profile lost its smooth, bell-shaped profile as elbow amplitude increased. This was particularly noticeable when wrist movements were combined with large-amplitude (70-deg) elbow movements (Fig. 4A, right). When small-amplitude wrist movements were combined with small-amplitude elbow movements, phasic activity in the agonist started prior to

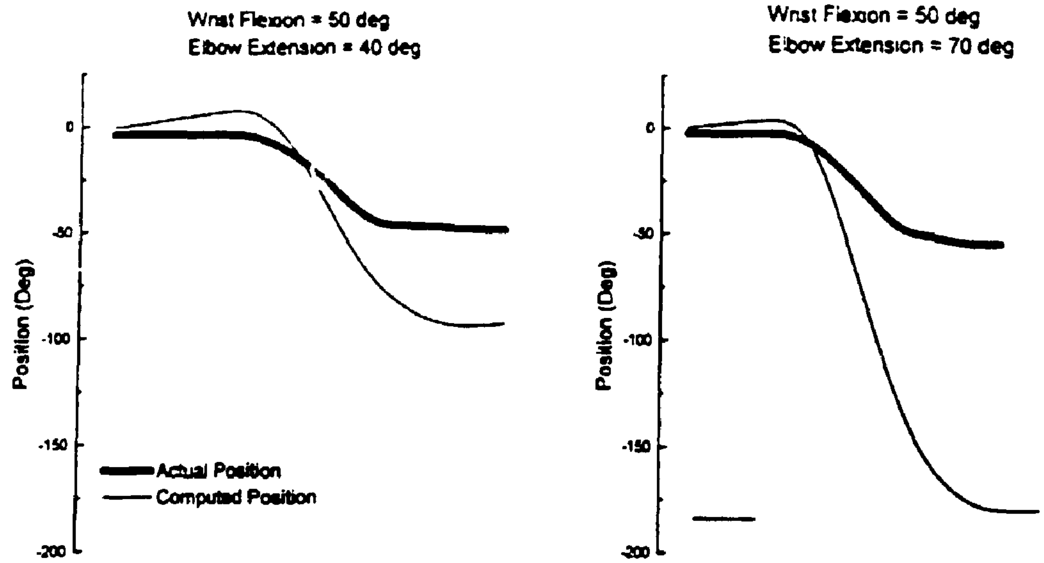

Fig. 5 Comparison of actual and computed wrist position. Records of wrist flexion movements of 50 deg (*thin traces*) combined with elbow extension movements of 40 and 70 deg were computed using the muscle torque from wrist movements of 50 deg combined with elbow extension movements of 10 deg. The actual wrist movements are also plotted for comparison (*thick traces*)

movement start (Fig. 4A, left). As the elbow amplitude increased, phasic activity in the *antagonist* occurred prior to movement start and was followed by phasic activity in the agonist. In addition, there was a qualitative increase in the magnitude of phasic antagonist activity with an associated qualitative decrease in agonist activity as elbow amplitude increased. When large-amplitude wrist movements were combined with small-amplitude elbow movements (Fig. 4B, left), phasic activation of the agonist was seen at the start of movement, similar to that observed in small-amplitude wrist movements. As elbow amplitude increased, the magnitude of phasic agonist activity decreased. In these movements there was no corresponding increase in antagonist activity. Thus the calculated changes in wrist muscle torque (reversal for small and a decrease for large wrist movements) corresponded directly to the observed changes in the pattern of muscle activation at the wrist joint.

Theoretical effect of maintaining the same wrist muscle torque

In order to assess the function of the changes in the EMG activation and resulting muscle torques, we computed the wrist movement which would result if the wrist muscle torques did not change as elbow amplitude increased. That is, we calculated what would happen to wrist movement if the increased reaction torques were not compensated for by altered wrist muscle torques. Wrist acceleration was computed for movements made with elbow amplitudes of 40 and 70 deg amplitude respectively. This acceleration was calculated from the actual reaction torques produced by elbow acceleration in each condition (under the assumption that wrist position was 50 deg), as well as the wrist muscle torque produced during 50-deg wrist movements combined with 10-deg elbow movements. Wrist position was then computed by double integration of the acceleration curve. Figure 5 shows the actual and computed movements for wrist flexion movements of 50 deg combined with elbow extension movements of 40 deg and 70 deg. With constant muscle torques about the wrist, the wrist movement would have increased from 50 deg to approximately 100 and 170 deg respectively. Clearly, compensation by decreasing agonist activity or by increasing antagonist activity was necessary to ensure that the correct movement amplitude would be achieved.

Discussion

Analysis of the relationship between movement kinematics and the underlying muscle activation pattern has long been a basic approach in understanding how the nervous system formulates motor commands to produce movement. Components of the triphasic pattern, typically observed in planar movements about a single joint (Brown and Cooke 1981; Hallett et al. 1975; Mustard and Lee 1987), are well correlated with explicit kinematic variables (Benecke et al. 1985; Berardelli et al. 1984; Brown and Cooke 1981, 1990; Cooke and

Brown 1994). While such relations can be very strong, it is likely that they arise because kinematic and kinetic characteristics of such movements covary. Thus, in such movements, EMG-kinematic relations are most likely reflective of EMG-force relations (e.g. Brown and Cooke, 1990; Cooke and Brown 1990; Hoffman and Strick 1990).

Such relationships, however, have not proven to be as direct in more complex movements. For example, single-joint movements made under different loading conditions may be associated with quite distinct patterns of muscle activity, although the movement trajectories are remarkably alike (Stein et al. 1988; Virji-Babul et al. 1994). A number of modifications have also been observed in the EMG-movement relations in multi-joint movements compared with the relations seen in planar, single-joint movements. For example, the magnitude of the initial agonist burst (Wadman et al. 1980), the time of onset of muscle activity (Flanders 1991) and the selection of muscle activity (Koshland and Hasan 1994) are thought to be dependent on movement direction. In addition, the initial muscle activity does not always correspond to the direction of joint rotation (Karst and Hasan 1991). These observed modifications are, in general, related to the force specifications of the task and are less directly associated with specific kinematic variables.

The paradigm used in this study was an extension of an earlier study (Virji-Babul and Cooke 1995) designed to evaluate the effects of elbow reaction torque directionality on wrist movement during a two-joint movement task. The results from our previous study demonstrated that when the two joints moved in the same direction, a basic pattern consisting of alternating bursts in the agonist and antagonist was observed at the wrist joint. This pattern was preserved despite changes in movement amplitude and target location. In the present study, with the same two joints moving in opposite directions, distinct patterns of muscle activation were observed at the wrist joint that were directly dependent on the magnitude of the reaction torques resulting from concurrent elbow acceleration. In conditions in which the magnitude of the elbow reaction torque was quite small, the wrist agonist was activated first. As the magnitude of the elbow reaction torque increased, two different strategies were used to account for these changing reaction torques at the wrist. If the elbow reaction torque greatly exceeded the net wrist torque, the wrist antagonist was activated first to oppose the reaction torque resulting from elbow acceleration. In such conditions, phasic activity in the wrist agonist followed the activity in the antagonist in order to counter the later reaction torque which acted in a direction to decelerate the movement. If the elbow reaction torque was approximately equal to the net wrist torque, the wrist agonist activity was decreased so that wrist movement was mainly driven by elbow reaction torques.

Taken together, these findings demonstrate that during two-joint planar movements, a systematic relationship exists between the force specifications of the task and the selection of muscle activation patterns used to produce movement of the distal joint. In conditions where motion of the proximal joint produces torques opposing movement of the distal joint (Virji-Babul and Cooke 1995), initial phasic activation is required in the wrist muscle normally termed the agonist. The magnitude of this activity would be dependent on the magnitude of the reaction torques, so that very large reaction torques opposing movement are counteracted by increasing phasic activity. In conditions in which motion of the proximal joint produces torques assisting movement of the distal joint, the selection of the muscle to be activated first is again dependent on the magnitude of the reaction torques. Initial phasic activity in the muscle generally termed as the antagonist would be required to compensate for large reaction torques in order to prevent excessively large movements from occurring.

Interestingly, in the present study, the pattern of muscle activation selected did not serve to preserve specific kinematic characteristics of the distal joint. Although wrist motion was generally characterised by a bell-shaped velocity profile, the wrist trajectory usually became more variable and less time symmetric as the elbow amplitude increased and the resulting reaction torques became greater in magnitude. Variability in wrist motion has been observed during other multi-joint movements, and it has been proposed that wrist motion may not be linked to movement of the proximal joints and may, in fact, be controlled independently from the more proximal joints (Lacquaniti and Soechting 1982; Soechting 1984). However, similar kinematic changes have been reported at the elbow during two-joint movements involving the shoulder and elbow joints (Kaminski and Gentile 1989), suggesting that this may be a common feature characterising motion of the distal joint.

Based on the results of this and our previous study, we suggest that wrist motion is linked very closely with elbow motion. The selection of muscle activation patterns at the wrist appears not to be simply dependent on target direction, but also on the relative magnitude and direction of the elbow reaction torques in relation to the desired wrist motion. Our findings indicate that motion of the elbow joint is an important consideration in planning wrist movements. Thus, movements of the distal joint may be planned globally at the kinematic level, with the variables of primary importance related to the net forces acting at the wrist joint.

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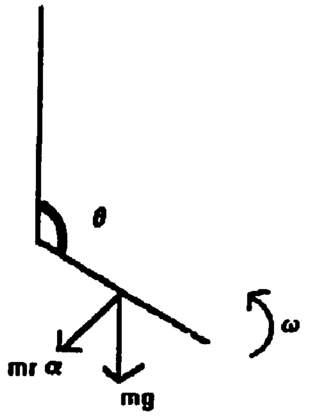
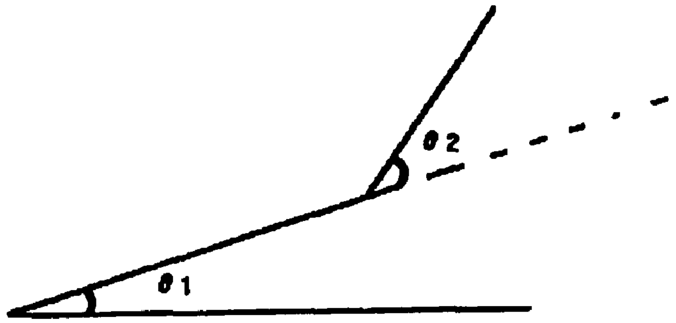
APPENDIX 4
Free Body Diagrams for Single and Two-Joint Movements

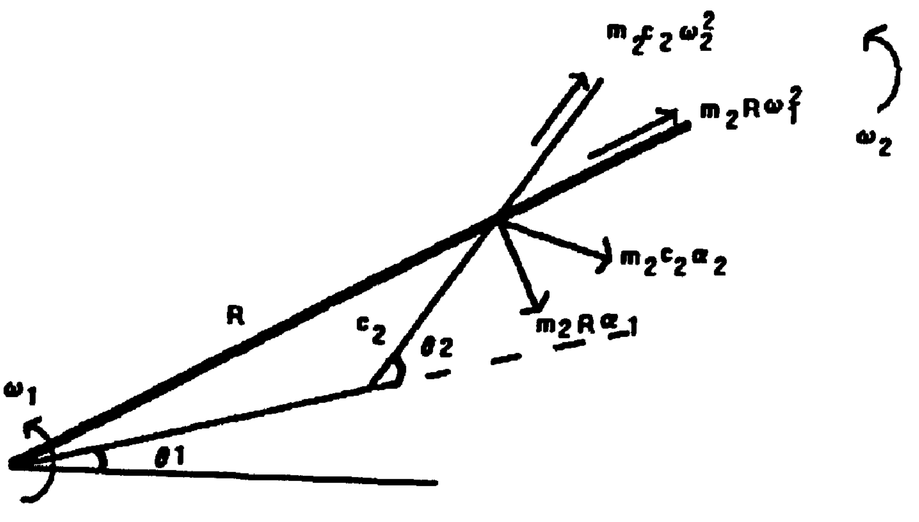
1. Free Body Diagram for Single Joint Movement:



2. Convention for defining joint angles - Two-joint movement:



3. Free body diagram for segment 2 (wrist):



APPENDIX 5

Estimates of segment mass and inertial characterstics of the hand segment for a typical subject

(Dempster's estimates reported in Winter (1991) were used for the calculations)

Total body Weight = 83 Kg
Length of wrist segment = .08m
I of the manipulandum = .006 kg.m^2

Mass of the hand (.006 X total body weight) = .5 kg
Radius of gyration/segment length = .297 (C of gravity)
Center of mass/segment length = .506 (proximal end)

$$I = I_o + mx^2$$

I_o = moment of inertia about the center of mass = $m\rho^2$

$$= (.5)(.08 \times .297)^2 = .0003 \text{ kg.m}^2$$

$mx^2 = (.5)(.08 \times .506)^2 = .001 \text{ kg.m}^2$

$I = (.0003 + .006) + (.001 + .006) = .01 \text{ kg.m}^2$

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