

RESEARCH ARTICLE

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Coordination of multiple muscles in two degree of freedom elbow movements

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Abstract The present study quantifies electromyographic (EMG) magnitude, timing, and duration in one and two degree of freedom elbow movements involving combinations of flexion-extension and pronation-supination. The aim is to understand the organization of commands subserving motion in individual and multiple degrees of freedom. The muscles tested in this study fell into two categories with respect to agonist burst magnitude: those whose burst magnitude varied with motion in a second degree of freedom at the elbow, and those whose burst magnitude depended on motion in one degree of freedom only. In multiarticular muscles contributing to motion in two degrees of freedom at the elbow, we found that the magnitude of the agonist burst was greatest for movements in which a muscle acted as agonist in both degrees of freedom. The burst magnitudes for one degree of freedom movements were, in turn, greater than for movements in which the muscle was agonist in one degree of freedom and antagonist in the other. It was also found that, for movements in which a muscle acted as agonist in two degrees of freedom, the burst magnitude was, in the majority of cases, not different from the sum of the burst magnitudes in the component movements. When differences occurred, the burst magnitude for the combined movement was greater than the sum of the components. Other measures of EMG activity such as burst onset time and duration were not found to vary in a systematic manner with motion in these two degrees of freedom. It was also seen that several muscles which produced motion in one degree of freedom at the elbow, including triceps brachii (long head), triceps brachii (lateral head), and pronator quadratus displayed first agonist bursts whose magnitude did

not vary with motion in a second degree of freedom. However, for the monoarticular elbow flexors brachialis and brachioradialis, agonist burst magnitude was affected by pronation or supination. Lastly, it was observed that during elbow movements in which muscles acted as agonist in one degree of freedom and antagonist in the other, the muscle activity often displayed both agonist and antagonist components in the same movement. It was found that, for pronator teres and biceps brachii, the timing of the bursts was such that there was activity in these muscles concurrent with activity in both pure agonists and pure antagonists. The empirical summation of EMG burst magnitudes and the presence in a single muscle of both agonist and antagonist bursts within a movement suggest that central commands associated with motion in individual degrees of freedom at the elbow may be superimposed to produce elbow movements in two degrees of freedom.

Key words Motor control · Arm movement · EMG · Coordination · Kinematics · Human

Introduction

The performance of arm movements requires the coordination of a number of muscles, both mono- and multiarticular, acting across a number of joints. The electromyographic (EMG) correlates of these movements have been studied extensively in the context of single-joint or single-degree-of-freedom arm motion, but only recently have these lines of work been extended to multi-joint or multi-degree-of-freedom movements. Studies of the relationship between muscle activity and movement kinematics in multi-degree-of-freedom movements have been of two general types: examinations of motor unit recruitment and EMG activity during isometric force production in two degrees of freedom (Buchanan et al. 1986; Jamison and Caldwell 1993; Jongen et al. 1989; Tax and Gielen 1993; van Zuylen et al. 1988) and examinations of kinematics and EMG activity during isotonic move-

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ments involving rotations about more than one joint (Flanders 1991; Karst and Hasan 1991). Both types of study have shown that parameters associated with EMG activity (e.g., motor unit recruitment threshold, EMG activity magnitude, EMG activity timing) may be dependent on motion in more than one degree of freedom. The present study extends this line of work by examining both the magnitude and the timing of EMG activity during elbow movements involving flexion-extension, pronation-supination, and combinations of the two. The relationships between movement kinematics and the associated EMG activity parameters are quantified. The aim is to assess the organization of commands to the elbow muscles that subserve motion in individual degrees of freedom and their combination.

A number of studies have investigated elbow torques involving combinations of isometric pronation-supination and flexion-extension. These studies have reported distinct motor unit subpopulations whose recruitment thresholds depend on torques in two degrees of freedom. As an example, biceps brachii recruitment thresholds for flexion torques decreased during the simultaneous production of a supination torque. There were also motor units in these muscles whose activity was not modulated by torque exerted in a second degree of freedom. For example, supinator contained only single degree-of-freedom units (van Zuylen et al. 1988). Motor unit subpopulations which can be defined on the basis of torques in two degrees of freedom have been reported in biceps brachii, triceps brachii, brachialis, brachioradialis and pronator teres (Jongen et al. 1989; Tax and Gielen 1993).

In addition to studies which have examined individual motor units, studies have been reported in which isometric torque production is related to overall EMG activity. Torques in one degree of freedom have been found to affect the magnitude of the EMG signal during simultaneous torques in a second degree of freedom (Buchanan et al. 1986; Jamison and Caldwell 1993). As an example, Jamison and Caldwell report that pronation or supination torques have a significant effect on EMG amplitude in biceps brachii and brachioradialis, but not in triceps brachii, during a maximum isometric flexion torque.

Synergistic relationships between muscles also change with torques in a second degree of freedom. Jamison and Caldwell (1993) report that biceps brachii activity increases during a combined flexion-supination torque and decreases during a flexion-pronation torque. Brachioradialis displays the opposite pattern; its activity increases during a flexion-pronation torque. This is presumably to compensate for the reduced biceps brachii contribution. It is interesting to note that the magnitude of brachioradialis activity is affected by a pronation-supination torque, since it is a monoarticular muscle which exerts torque primarily in the flexion-extension direction. The finding that synergistic action varies with torque direction has also been reported by Buchanan et al. (1986) in the context of isometric torques produced simultaneously in the flexion-extension and varus-valgus directions.

In the present experiment, subjects perform elbow movements involving various combinations of flexion-extension and pronation-supination. We assess patterns of muscle activity when a muscle acts as agonist in two degrees of freedom, as agonist in one degree of freedom only, and as agonist in one degree of freedom and antagonist in the other. We quantify various EMG signal parameters – burst onset, magnitude, and duration – associated with movements in one and two degrees of freedom about the elbow. Relationships between the amplitude of motion in each degree of freedom and the associated EMG signals are assessed with the goal of understanding the associated neural commands subserving these movements.

Materials and methods

The experimental procedures used in these studies have been approved by the McGill University Department of Psychology ethics committee. All subjects gave their informed consent prior to each experiment.

Procedure

Subjects made forearm movements to targets in a sagittal plane. The movements involved flexion or extension alone, pronation or supination alone, and combinations of the two. EMG patterns associated with these movements were recorded from eight single- and double-joint muscles. Arm position was recorded in three dimensions using Optotrak (Northern Digital).

Figure 1 shows the experimental setup and the arm position conventions used. In movements involving flexion or extension alone the forearm was either fully pronated or fully supinated. The flexions started with the elbow fully extended and were either 70° or 140° in magnitude. Start and end positions were reversed for extension movements. Thus there were a total of eight movement conditions involving flexion or extension alone: two directions × two magnitudes × forearm prone or supine.

In movements involving pronation or supination alone, the elbow was either fully extended (-90°) or flexed 50°. The movements consisted of 70° and 140° pronations and 70° and 140° supinations (starting positions were forearm fully supinated and fully pronated, respectively). Thus, in total, there were eight pronation-supination movement conditions.

In movements combining flexion-extension with pronation-supination, subjects started with the elbow fully extended (flexion movements) and the forearm either fully pronated or fully supinated. Subjects flexed the arm either 70° or 140° while simultaneously supinating or pronating either 70° or 140°. Start and end positions were reversed for extension movements. All combinations of the two magnitudes in each of the two degrees of freedom and in both directions were performed for a total of 16 movement conditions.

Five subjects were tested with the upper arm held vertically. An additional three subjects were tested with the upper arm in a horizontal position. In order to insure that movements were limited to the two degrees of freedom about the elbow, a brace was used to restrict wrist motion. Subjects were instructed to keep the upper arm stationary. The upper arm position was monitored during the experiment and trials were repeated if there was upper arm movement.

For all eight subjects described above, an audiometronome was used to maintain movement duration at 350 ms. Four additional subjects were tested, with the upper arm both vertical and horizontal, under conditions where timing was not explicitly controlled. These subjects were simply instructed to move quickly. A prelimi-

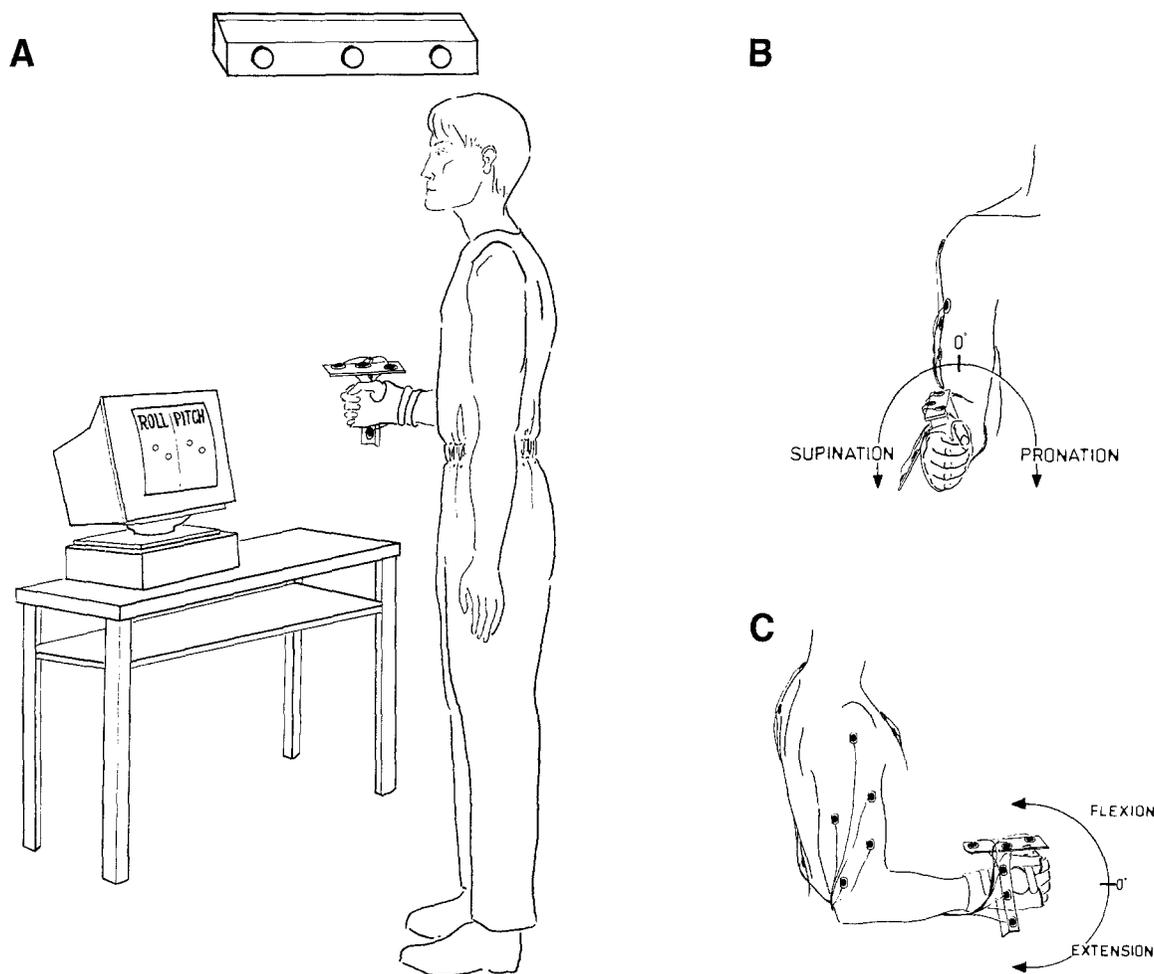


Fig. 1 **A** Schematic of the experimental setup. Subjects face a video monitor displaying targets in each degree of freedom. A Plexiglas apparatus with attached infrared-emitting diodes (IREDs) allows Optotrak to monitor forearm orientation and position. **B** Reference position for forearm pronation-supination; 0° corresponds to the arm held in a semiprone position. Pronation angles are positive, supination are negative. **C** IRED placement on the upper arm and on the forearm apparatus. Reference position for forearm flexion-extension; 0° corresponds to the forearm held horizontal and the upper arm held vertical and in a parasagittal plane. Flexions are positive, extensions are negative

nary analysis of this latter study was reported in Sergio and Ostry (1994).

In total, 320 trials (10 trials for each of 32 conditions) were collected for each subject. Subjects were allowed rest periods. Subjects practiced each movement until the movement could be performed smoothly while starting and ending within the targets for each degree of freedom. The target zones were displayed separately on a video monitor for each degree of freedom (see Fig. 1A and the section on movement targets).

During movements involving both one and two degrees of freedom at the elbow, multiarticular muscles may act as agonist in one degree of freedom and as antagonist in the second. A further study was run in order to assess the conditions under which multiarticular muscles display either agonist or antagonist activity. Five subjects performed four different sets of discrete movements. In each movement condition, the amplitude of the movement in one degree of freedom was fixed, while the amplitude in the other degree of freedom was gradually increased. The four movements were: fixed amplitude flexion (90°) with a continually increasing supination (10° – 130°), fixed amplitude flexion with a continually in-

creasing pronation, fixed amplitude pronation (100°) with a continually increasing flexion, and fixed amplitude supination (125°) with a continually increasing flexion. Twenty discrete movements were collected in each condition. The forearm was in all cases held at an initial flexion angle of -70° .

Muscle activity recording

EMG activity patterns were recorded from muscles about the elbow using bipolar surface electrodes (Neuromuscular Research Center). Each electrode consisted of two 1-by-10-mm parallel silver bars placed 10 mm apart. The electrodes were housed in a compact, lightweight case containing a $\times 10$ preamplifier. Recordings were made from the following eight muscles: triceps brachii (long head), triceps brachii (lateral head), biceps brachii (long head), biceps brachii (short head), brachialis, brachioradialis, pronator teres, and pronator quadratus. EMG signals were sampled at 1200 Hz, band-pass filtered between 20 and 300 Hz, rectified, and integrated off-line.

Electrode placement was verified by having subjects perform test maneuvers. The placement for a number of muscles warrants comment. Pronator quadratus is situated underneath wrist tendons and both pronator teres and brachialis are situated near large wrist and elbow flexor muscles. Hence, specific procedures were employed to control the placement of electrodes for these muscles in order to ensure that the desired muscle activity was recorded. Figure 2C displays the activity of pronator teres and pronator quadratus during pronation, finger flexion, and wrist flexion. Pronator teres showed no activity during finger or wrist flexion. Electrodes recording pronator quadratus activity displayed a large spiking activity pattern (presumably due to the motion of tendons) during finger or wrist flexion. This pattern was easily distinguishable on

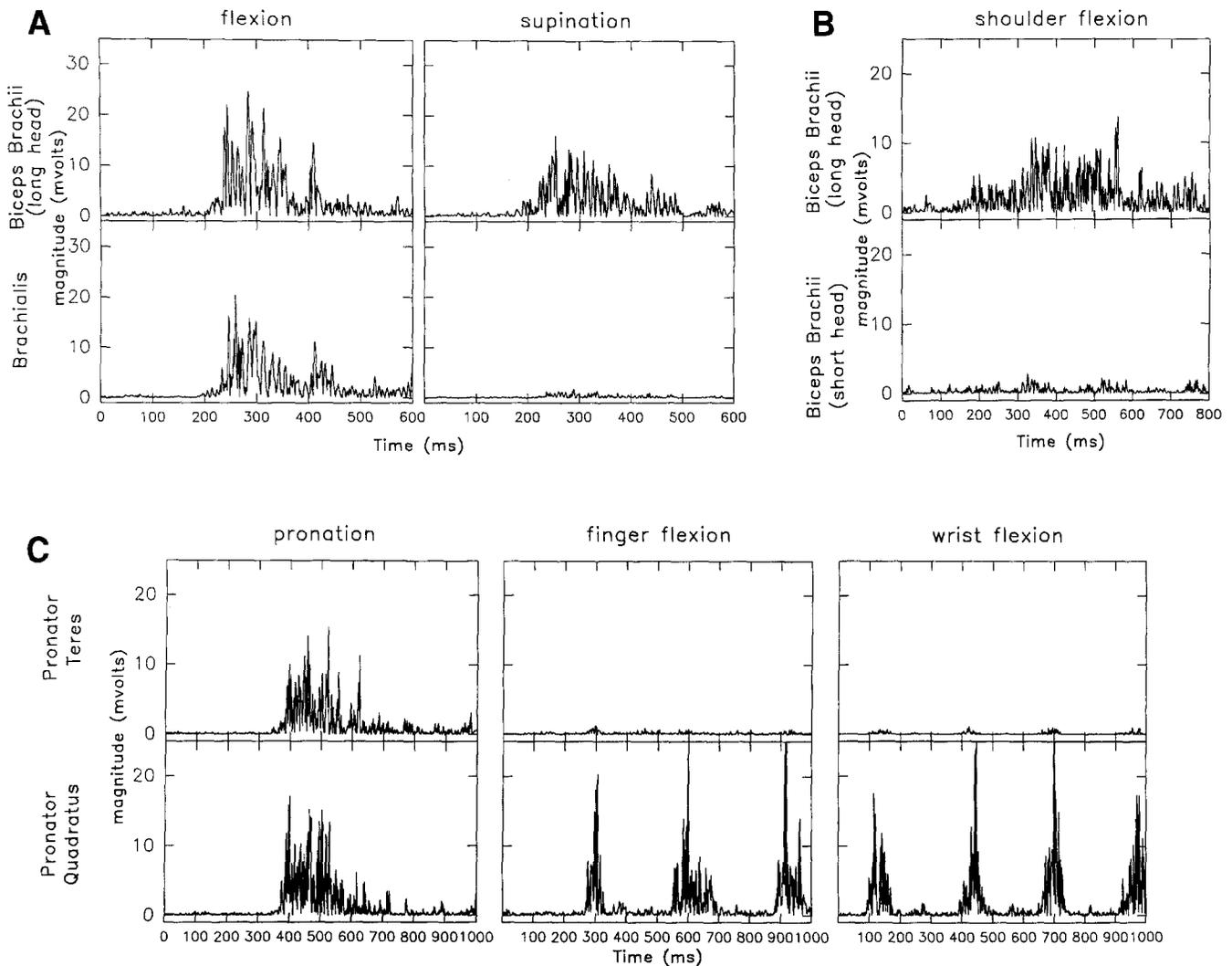


Fig. 2A–C Tests for surface electrode placement. **A** Brachialis shows a burst of activity during flexion, but not during supination. **B** Biceps brachii (long head) displays greater activity during a sustained shoulder flexion than biceps brachii (short head). **C** Pronator teres shows little activity during finger or wrist flexion. Pronator quadratus displays readily identifiable large spikes of activity during finger or wrist flexion. Data are shown for subject 1

the basis of both amplitude and time course from the actual muscle activity pattern. Brachialis could be distinguished from biceps brachii as a muscle which produced activity during flexion only and not during supination (Fig. 2A). The long and short heads of biceps were also readily distinguishable during tests involving shoulder flexion (Fig. 2B). During experimental trials, the wrist was stabilized using a metal splint which was held in position using an elastic brace with Velcro straps. This effectively eliminated any wrist flexion movement.

Movement recording

The position of the arm was recorded in three dimensions using an Optotrak system. Infrared-emitting diodes (IREDs) were placed on the subject's upper arm and on a lightweight Plexiglas apparatus strapped to the wrist (Fig. 1). Five to six IREDs were used to define each structure; their positions were sampled at 100 Hz.

The static positions of IREDs relative to anatomical landmarks were recorded for later calculation of the orientation angles of the

upper and lower arm. Specifically, three-dimensional (3D) distances between the acromion and upper arm markers and between the olecranon and lower arm markers were measured. Using these known distances, forearm orientations were calculated in an elbow-centered coordinate system.

Movement targets

A real-time viewing program displayed the targets, the current forearm elevation in the sagittal plane, and current forearm pronation-supination in the frontal plane. Subjects made movements to align the current forearm position with the circular targets (Fig. 1A). The target positions were calculated individually for each subject while the arm was in each of the desired start and end configurations. The targets consisted of a circle with a diameter corresponding to 15° in either the pitch (flexion-extension) or roll (pronation-supination) orientation.

Kinematic analysis

The orientation angles of the lower arm were calculated from raw data using rigid body reconstruction techniques based on the method of quaternions (Horn 1987). Lower arm motion was specified relative to the upper arm. Orientation angle records were numerically differentiated by use of the least squares method (Dahlquist and Björck 1969). Kinematic records were scored for movement start and end using 10% of the maximum velocity.

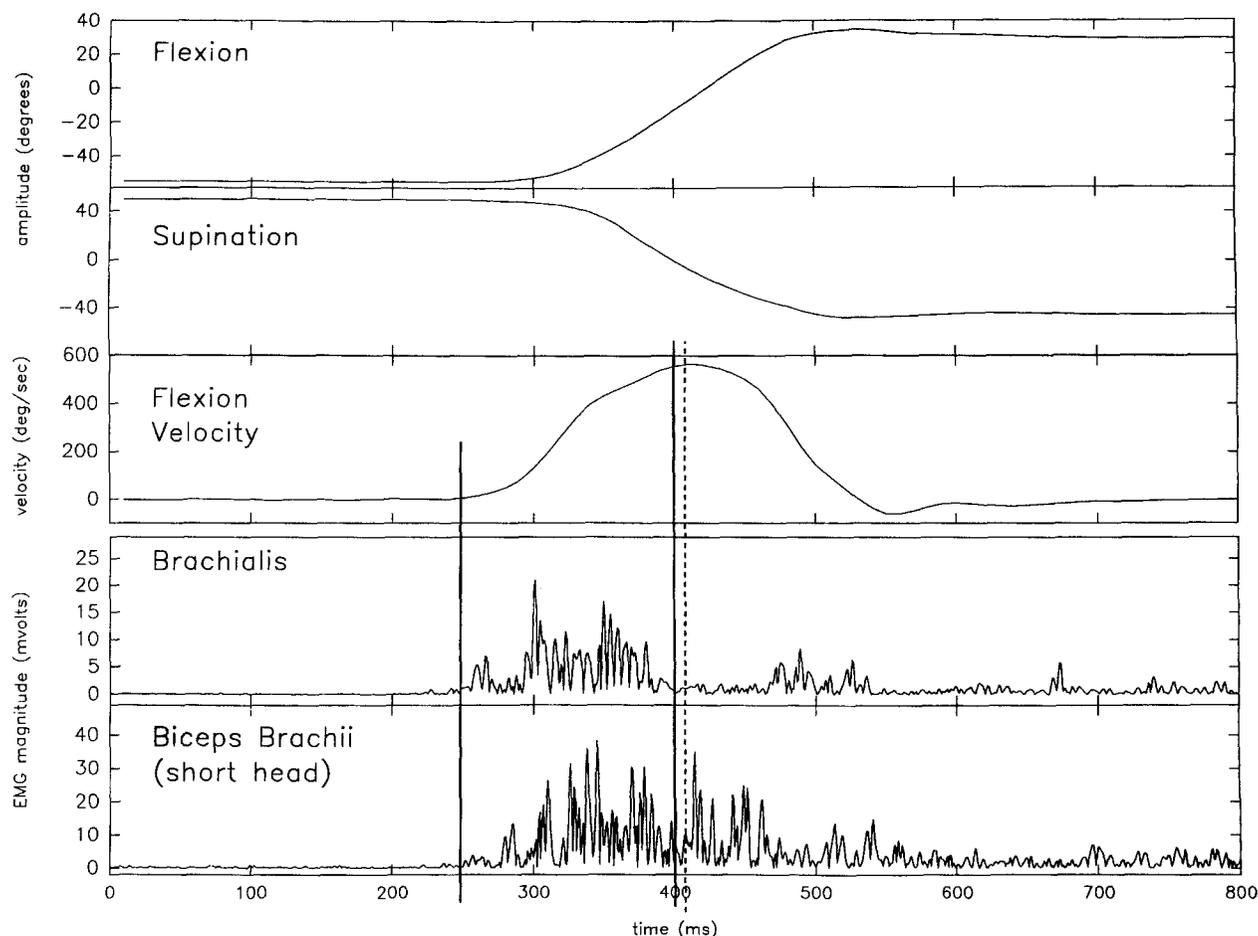


Fig. 3 Kinematic and EMG activity records showing scoring procedures. Vertical solid lines indicate start and end of brachialis activity at points 2 SDs above the baseline EMG activity. The vertical dashed line is the point of burst end scored by using the peak flexion velocity. The two methods differ in scoring burst end by 5 ms. Data are shown for subject 3

EMG analysis

EMG signals were scored for the start and end of the first burst of activity displayed by a muscle. This first burst of activity could be either the first agonist burst or the first antagonist burst, depending on the muscle. Burst onset was scored as the point on the EMG record 2 SDs above a baseline level prior to movement onset. The baseline region was selected on a trial-by-trial basis using an interactive computer program. The baseline region was typically 200–300 ms in duration. The end of the burst was scored as the point at which the EMG signal returned to baseline (see below). A numerical estimate of the burst magnitude was obtained by calculating, using Simpson's rule, the integrated area under the rectified EMG signal between the point of burst start and end.

In 10–20% of trials in which flexion-extension was combined with pronation-supination, muscles which acted as agonist in both one and two degrees of freedom (e.g., biceps in combined flexion-supination) displayed an EMG activity pattern that did not return to baseline until the end of the movement. In other, similar trials, where EMG did return to baseline, the end of the first agonist burst corresponded closely to both the onset of antagonist activity and the peak velocity of movement in either the flexion or supination degree of freedom. Thus, for purposes of data analysis, the end of the burst was scored at the point of peak velocity in trials which displayed an extended agonist burst. For all trials, burst start and end were visually verified to ensure that the algorithms

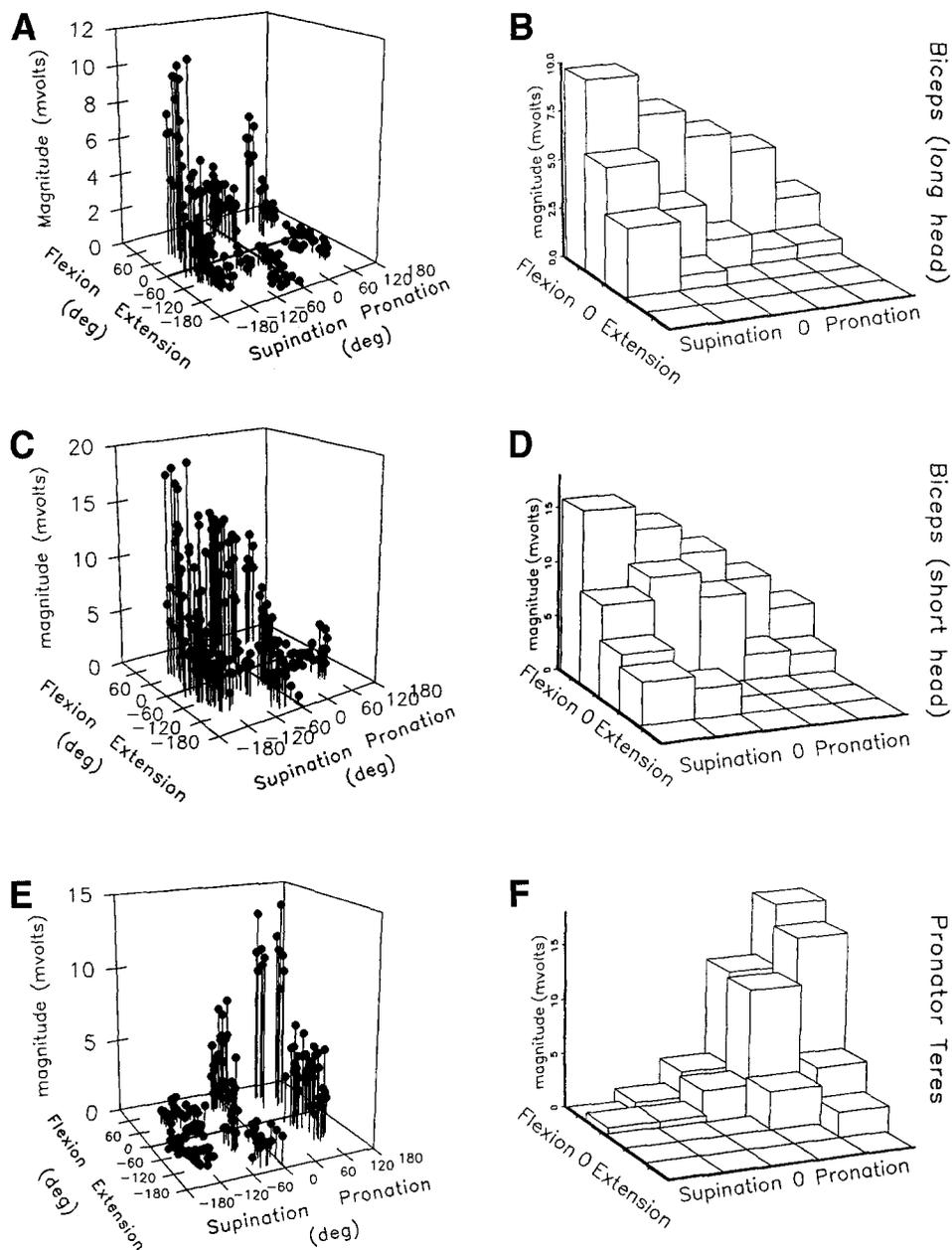
reached reasonable solutions. However, it should be noted that the computerized algorithms produced reasonable results in the majority of cases.

Figure 3 displays position, velocity, and EMG activity records for a flexion-supination movement. The agonist bursts are well defined for the brachialis but less so for the short head of biceps brachii. A comparison between scoring on the basis of standard deviations and peak velocities is shown. The solid lines indicate the burst start and end scored by measuring the point two standard deviations above the EMG baseline level. The dashed line indicates where the end of the burst would be scored using the point of peak flexion velocity. It can be seen that in this example there is a 5-ms difference between the two criteria. Other examples yielded comparable results.

Results

In this section we assess EMG magnitude, timing, and duration in mono- and multiarticular elbow muscles. We examine the effect of varying the amplitude of motion in one and two degrees of freedom. We show, for multiarticular muscles, that the agonist burst magnitude for motion in two degrees of freedom is, in general, not different from the sum of the burst magnitudes in the component one-degree-of-freedom movements. When differences occur, the sum is greater than the component one-degree-of-freedom magnitudes. We show, in addition, that multiarticular muscles often display both agonist and antagonist components in the same movement, when

Fig. 4A–F Agonist EMG magnitudes for multiarticular elbow muscles. **A,C,E** Agonist burst magnitudes for combinations of elbow flexion-extension, pronation-supination. Each *dot* represents an individual trial. Pitch and roll axes indicate the amplitude of movement in each degree of freedom. **B,D,F** Mean agonist burst magnitudes for panels **A,C**, and **E**, respectively. Each block represents the mean burst magnitude (across ten trials) for each movement condition. Data shown are from subject 3 for trials in which movement time was explicitly controlled



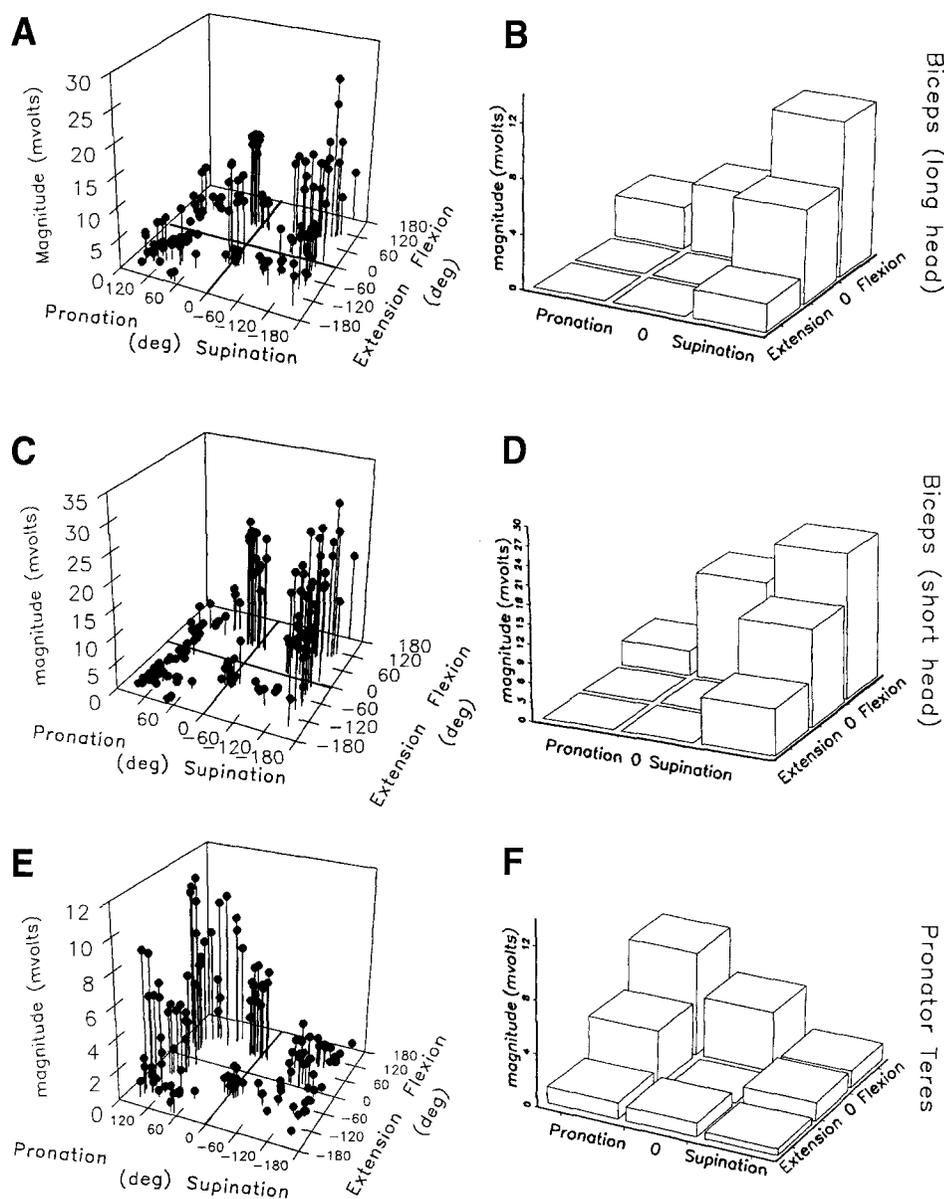
the muscle acts as agonist in one degree of freedom and antagonist in the other.

Magnitude of first agonist burst

Muscles could be classified into two categories with respect to the magnitude of the first agonist burst. Multiarticular muscles such as biceps brachii (long head), biceps brachii (short head), and pronator teres showed activity that was affected by motion in two degrees of freedom. The magnitude of the burst was greatest for movements in which the muscle acted as an agonist in both one and two degrees of freedom, less for one-degree-of-freedom movements, and less still for movements in which the muscle was agonist in one degree of

freedom and antagonist in the other. As an example, Fig. 4A,B shows, for a single subject, the magnitude of the biceps brachii first agonist burst for different amplitudes of flexion-extension and pronation-supination. The panels to the left give the burst magnitude for individual trials. The panels on the right show mean magnitudes for each movement condition. The data shown in this figure are for trials in which timing was explicitly controlled. It can be seen that the magnitude of the burst is greatest for flexing supinations where the muscle acts as an agonist for both flexion and supination. The magnitude is smaller for flexions alone and supinations alone, and it is smallest for flexing pronations and extending supinations. Similar patterns are observed for biceps brachii (short head) and pronator teres. Figure 5 shows, for a different subject, the pattern of activity in

Fig. 5A–F Agonist EMG magnitudes for multiarticular elbow muscles. Panels on the *left* display individual trials. Panels on the *right* display data averaged for each movement condition. Data shown are from subject 5 for trials in which movement time was not explicitly controlled



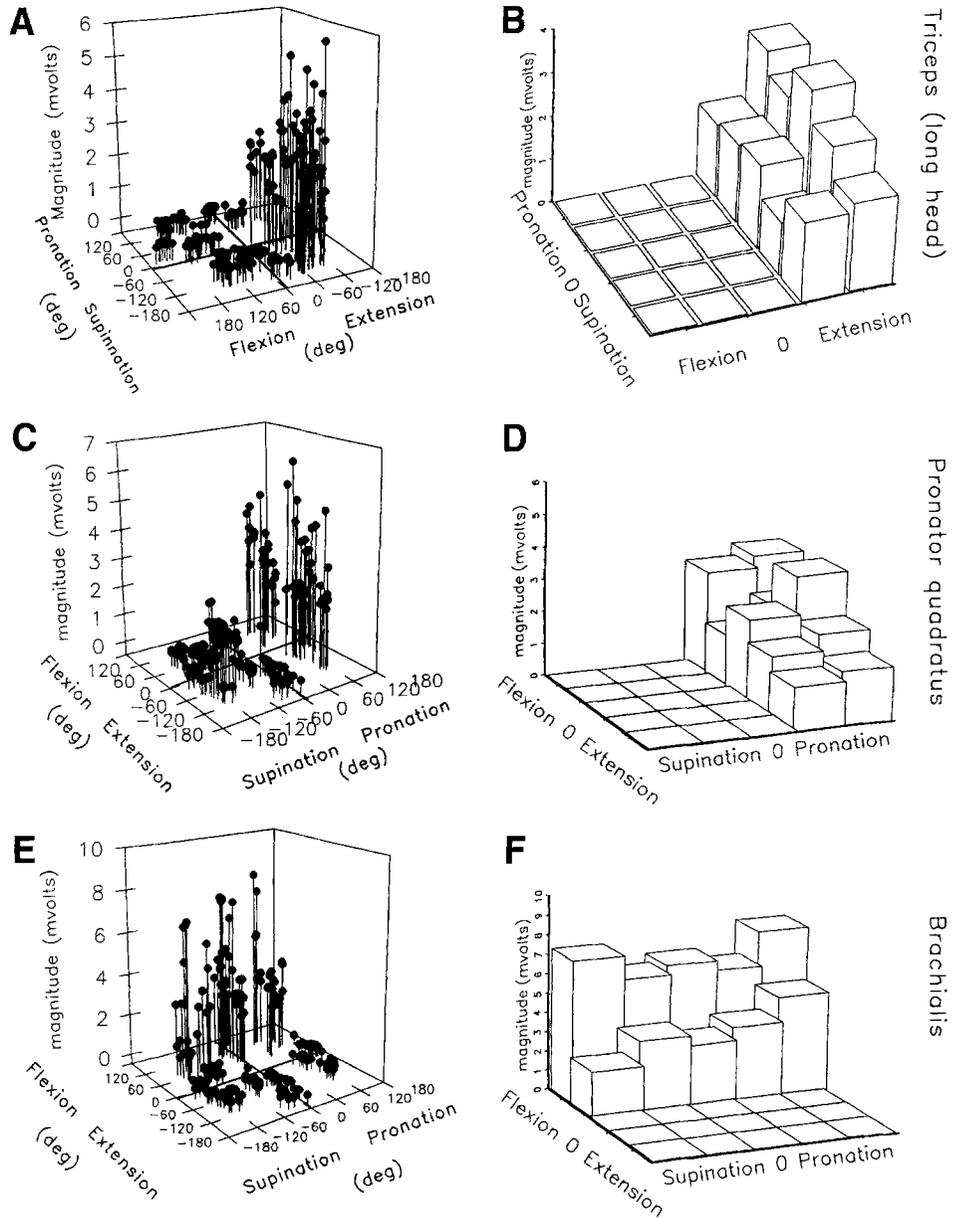
these same three muscles when timing was not explicitly controlled. Once again, it can be seen that the magnitude of the first agonist burst is graded over motion in the two degrees of freedom.

A statistical comparison of first agonist burst magnitudes was performed for each subject using a one-way ANOVA. When multiarticular muscles acted as agonist in two degrees of freedom, the magnitude of the first agonist burst was greater than in all other conditions ($P < 0.01$). In addition, in movement conditions in which the muscle acted as agonist in one degree of freedom only, the agonist burst magnitudes were greater than when the muscle acted as agonist in one degree of freedom and antagonist in the second ($P < 0.01$). Similar statistical results were obtained for all subjects and for all multiarticular muscles that we have examined.

In movements in which a muscle acted as agonist in two degrees of freedom, the magnitude of the agonist

burst was not, in the majority of cases, different from the sum of the agonist burst magnitudes of the component one-degree-of-freedom movements. This idea was tested statistically using Scheffé post hoc contrasts. Owing to the nature of statistical testing, we were able to test only for departure from the summation of component EMG burst magnitudes, rather than for summation itself. Tests for departure from summation were done both for subjects who performed the experiment under explicit timing conditions and those for whom timing was not controlled. Similar statistical results were obtained in both conditions. Overall, seven out of nine subjects showed no departure from summation of component EMG magnitudes for either the long or the short head of biceps brachii ($P > 0.01$). For pronator teres five out of nine subjects showed a similar pattern ($P > 0.01$). In all cases in which the component EMG magnitudes did not empirically summate, the sum of the two components was al-

Fig. 6A–F Agonist EMG magnitudes for muscles producing one-degree-of-freedom elbow movement. Panels on the *left* display individual trials. Panels on the *right* display data averaged for each movement condition. Data shown are from subject 3 for trials in which movement time was explicitly controlled. (Note that, for this subject, brachialis burst magnitude depends on motion in one degree of freedom. In other subjects, brachialis magnitude depends on motion in two degrees of freedom. See text)



ways less than the magnitude in the two-degree-of-freedom condition.

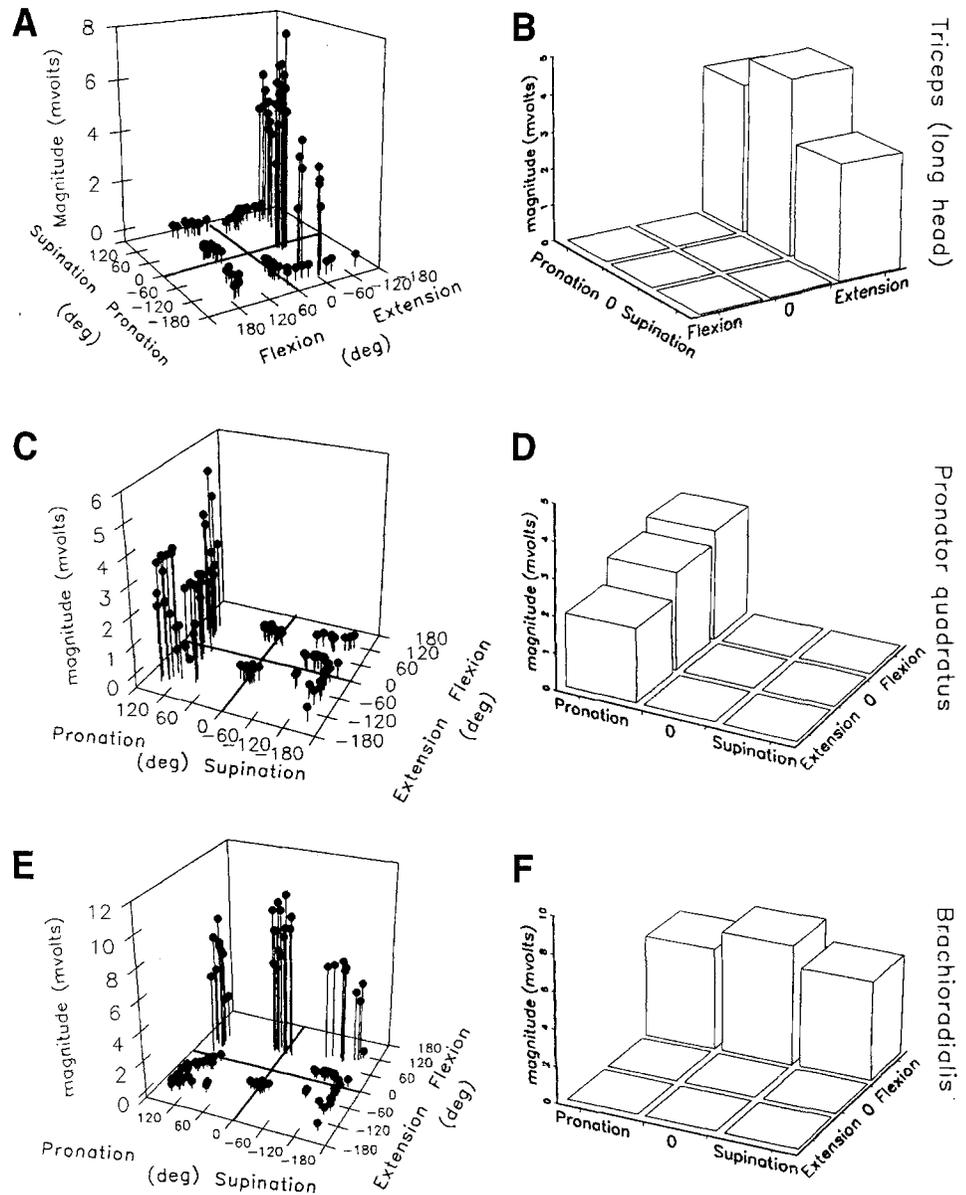
Muscles producing motion in one degree of freedom at the elbow, including triceps brachii (long head), triceps brachii (lateral head), and pronator quadratus, had first agonist bursts whose magnitude did not vary with motion in a second degree of freedom. For example, triceps brachii (long head) displayed a first agonist burst whose magnitude was essentially constant over extension movements of a given amplitude regardless of the amount of accompanying motion in the pronation or supination direction. Representative patterns are shown in Fig. 6 for one subject, under conditions of explicit timing, and in Fig. 7 for a second subject for trials in which timing was not controlled. (It should be noted that while the magnitude of triceps brachii burst activity did not vary with motion in a second degree of freedom, there

was typically an increase in the tonic level of triceps brachii activity during pronation or supination movements.)

For triceps brachii (lateral and long head) and pronator quadratus, statistical comparisons revealed significant differences in agonist burst magnitude between large and small amplitude movements ($P < 0.01$). Motion in the second degree of freedom produced no significant differences in burst magnitude ($P > 0.01$). All subjects showed this statistical pattern for these muscles.

Activity in the monoarticular muscles brachialis and brachioradialis was affected by motion in a second degree of freedom. As seen in Fig. 8, the burst magnitude of brachioradialis (an elbow flexor) is greater for a flexing pronation (Fig. 8B) than for a flexing supination (Fig. 8A). This has also been observed in brachialis in other trials. Biomechanically, brachialis and brachioradialis produce torque primarily in the flexion direction.

Fig. 7A–F Agonist EMG magnitudes for triceps brachii, pronator quadratus, and brachioradialis. Panels on the *left* give individual trials. Panels on the *right* give data averaged for each movement condition. Data shown are from subject 4 for trials in which movement time was not explicitly controlled. (Here, brachioradialis burst magnitude depends on motion in one degree of freedom. For other subjects, the pattern of brachioradialis activity depends on motion in two degrees of freedom. See text and Fig. 8)



Given the reduction in biceps brachii activity during flexing pronations (Fig. 8), the increase in monoarticular flexor activity may occur as a compensatory measure.

For the elbow flexors brachialis and brachioradialis, agonist burst magnitude was affected by pronation-supination. In four out of five subjects, the burst magnitude was greater in flexing pronations than in flexing supinations ($P < 0.01$). However, a subject showed this pattern for only one muscle or the other. In two subjects, brachialis burst magnitude was greater for flexing pronations than for flexing supinations, while for two other subjects, the brachioradialis burst magnitude was greater.

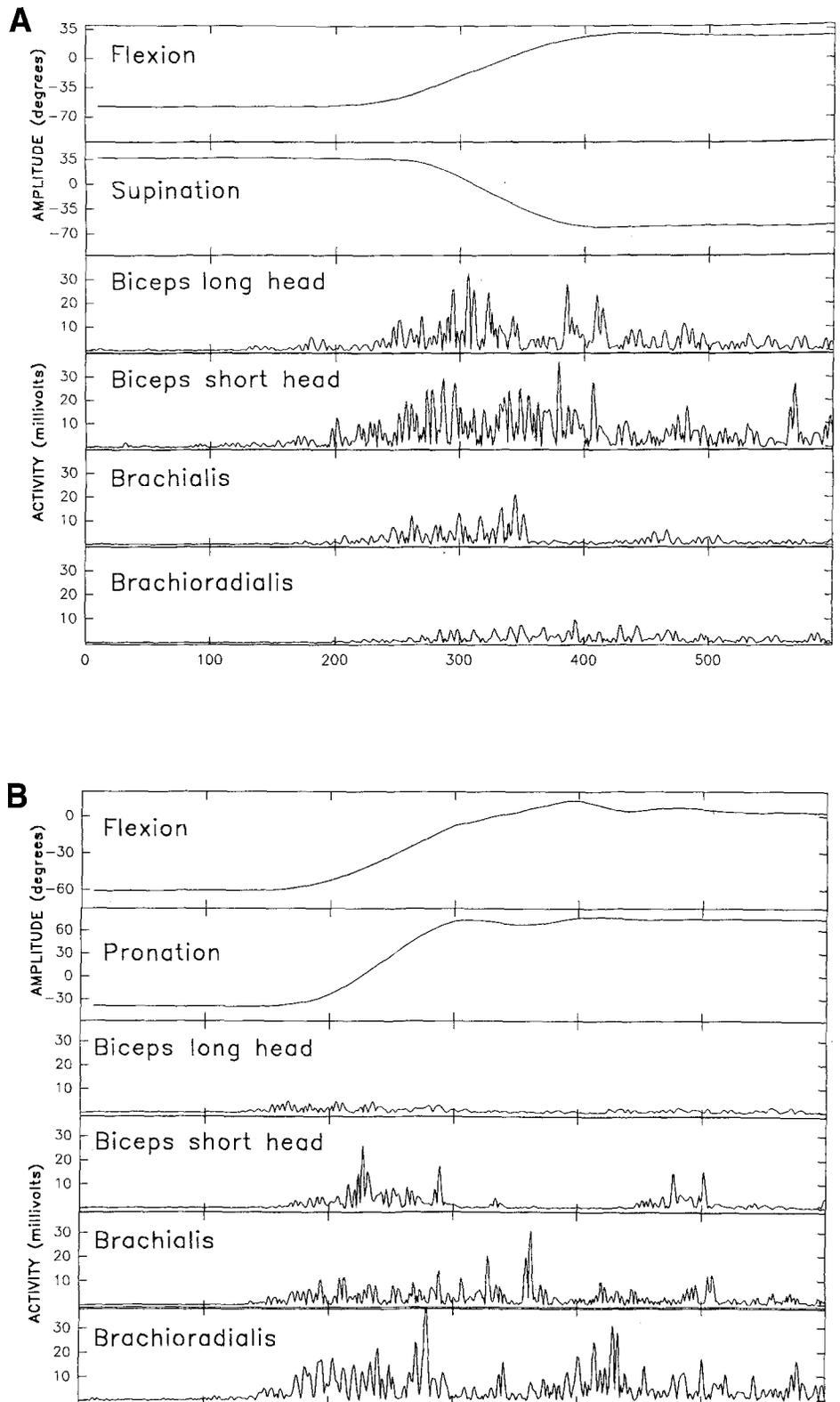
In the three subjects who performed the movements with the upper arm horizontal, the behavior of each of the muscles examined was the same as in the upper-arm-vertical condition, with the following exception: the absolute magnitude of the agonist burst changed for biceps brachii (long head) and triceps brachii (long head), both

of which act across the shoulder. In all three subjects, these muscles displayed a decrease in the magnitude of the agonist burst to a level lower than that of their single-joint counterparts (i.e., biceps brachii (short head) and triceps brachii (lateral head)) ($P < 0.01$). As a result, in two of three subjects the biceps brachii burst magnitude was *not* greater when it was acting as agonist in two degrees of freedom than in one degree of freedom ($P > 0.01$).

Behavior of multiarticular muscles during movements in two degrees of freedom

Muscles such as biceps brachii and pronator teres act in two degrees of freedom at the elbow. This creates a situation where a muscle may simultaneously act as an agonist and an antagonist. For example, during a flexing pronation the biceps brachii, which flexes and supinates

Fig. 8 Kinematic patterns and EMG activity for a movement combining flexion and supination (A) and flexion and pronation (B). Note that the level of brachioradialis (a monoarticular elbow flexor) activity relative to the level of biceps (long head) activity changes with motion in the pronation-supination degree of freedom. Data shown are from subject 5



the forearm, acts as an agonist to the flexion movement and an antagonist to the pronation movement. Under these circumstances, a number of possibilities exist concerning the activation patterns of these muscles. One possibility is that, in cases where the muscle could be either agonist or antagonist, it acts solely as one or the

other. An alternate possibility, and one which is supported in the present experiment, is that a muscle may display both agonist and antagonist components in its EMG pattern even within a single movement.

It was found that pronator teres and biceps brachii often displayed an activity pattern which had both agonist

and antagonist components. That is, the timing of the bursts was such that there was activity in these muscles that was concurrent with activity in both pure agonists and pure antagonists. Figure 9 shows the activity of various mono- and multiarticular muscles during four different, two-degree-of-freedom movements. Each panel shows data for a different subject. Figure 9A,B shows an extending supination and a flexing pronation. In these records, biceps brachii displays both agonist and antagonist activity. That is, there is activity coincident with both pure agonists and pure antagonists. Figure 9C,D shows a flexing supination and an extending pronation where in both cases pronator teres is both agonist and antagonist. Note for pronator teres that the magnitude of the EMG activity associated with pronation or supination is small. This is due to a general tendency for EMG magnitudes to be greater for flexion or extension movements than for equal-amplitude pronation or supination movements.

The presence of both agonist and antagonist bursts within the same movement was seen in all subjects for pronator teres, however, it was not present in all trials. For biceps brachii this pattern was seen in all but two of nine subjects, but again was not present in all trials. A detailed examination of the frequency of this behavior was undertaken for two subjects. For one subject, it was found that, in 69% of the trials involving flexing supination or extending pronation, pronator teres displayed both agonist and antagonist components. For this same subject, biceps brachii showed both agonist and antagonist activity in 39% of trials involving flexing pronation or extending supination. For a second subject, pronator teres displayed both agonist and antagonist components within a single movement in 55% of the trials where it was agonist to motion in one degree of freedom and antagonist in the second. Biceps brachii exhibited agonist and antagonist activity 40% of the time.

Burst onset relative to movement onset

The timing of muscle burst activity relative to arm movement onset was examined in two ways: the onset of activity for a given muscle across all movement conditions, and the onset of activity for a given movement condition across all muscles. Initially muscles were classified qualitatively as displaying agonist burst activity, antagonist burst activity, tonic activity, or no activity in each movement condition. Multiarticular muscles displaying both agonist and antagonist activity were classified according to which burst was larger in magnitude for purposes of this analysis. Muscles displaying agonist burst activity were subsequently analyzed separately from muscles displaying antagonist burst activity.

Burst onset relative to movement onset for a given movement condition across muscles

Both when movement timing was explicitly controlled through use of an audio metronome and when it was not

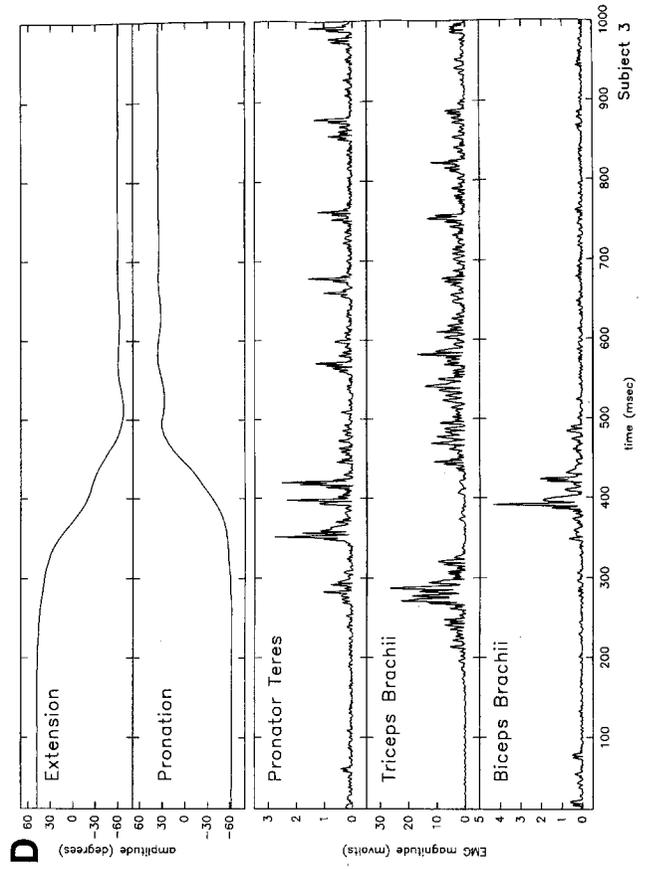
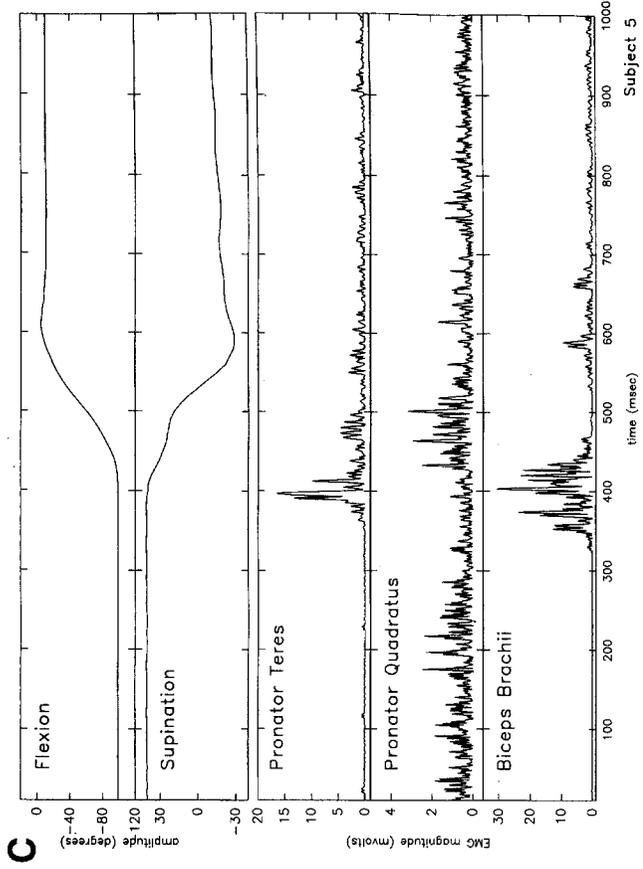
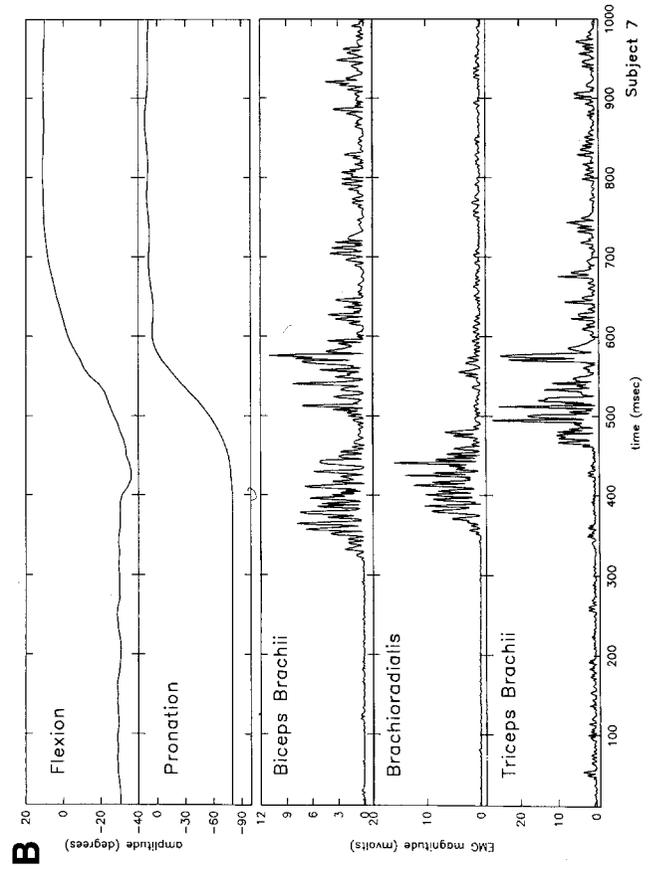
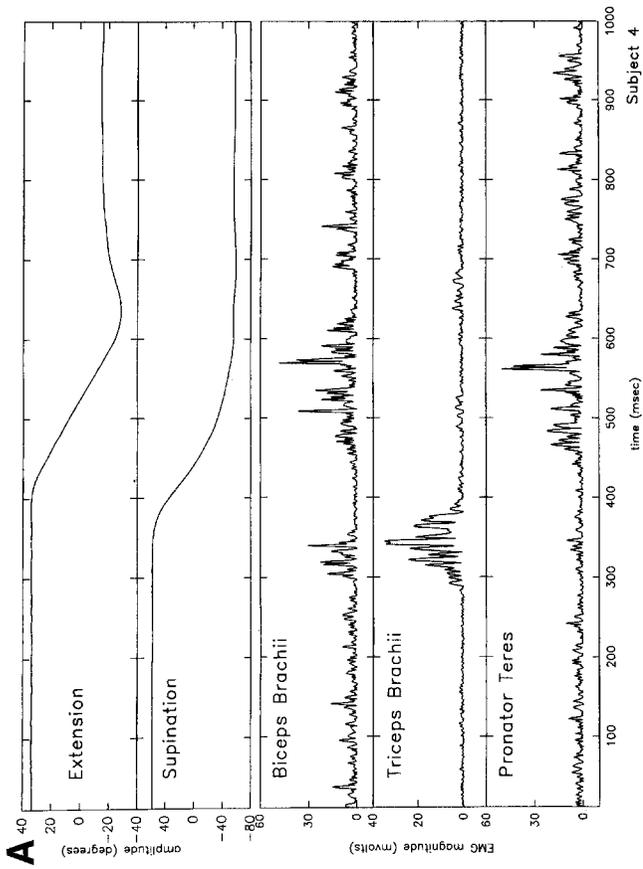
explicitly controlled, the pattern of EMG timing was similar. For a given discrete movement, no differences in muscle burst onset time were observed either for muscles acting as agonists or for muscles acting as antagonists ($P>0.01$, for both agonists and antagonists). All ten subjects tested in the two timing conditions as well as the three subjects tested with the upper arm held horizontally displayed this statistical pattern. As an example, during a flexing supination, biceps brachii (both long and short heads), brachialis, and brachioradialis all came on approximately 50 ms prior to movement onset, while triceps brachii (both long and lateral head) and pronator quadratus came on approximately 100 ms after movement onset. Figure 10 shows the onset time of the first agonist and antagonist bursts relative to the onset time of arm motion for three representative movements.

Burst onset relative to movement onset for a given muscle across movements

Individual muscles displayed burst onset times which did not vary across movement conditions in which the muscle acted as agonist ($P>0.01$, one-way ANOVA). Similarly, no differences among burst onset times were found when the muscle was classified as antagonist ($P>0.01$). This pattern held for all ten subjects tested in the two timing conditions as well as the three subjects who performed the experiment with the upper arm horizontal. Figure 11 shows burst activity onset times over different amplitudes of flexion-extension and pronation-supination for pronator teres, brachialis, and pronator quadratus. This behavior was seen in all muscles. When movement time was not explicitly controlled, although there were no significant differences in an individual muscles' burst onset times, the overall variability of onset times was greater. For example, the agonist burst onset mean and standard deviation for biceps brachii long head (subject 2) was -45 ± 20 ms when timing was explicitly controlled, and -47 ± 42 ms when it was not controlled. Other subjects showed comparable patterns.

Duration of muscle burst

To investigate the possibility that differences in EMG burst magnitudes were due to differences in burst duration, we examined the duration of muscle bursts, both agonist and antagonist, in different movement conditions. Within a condition, the duration of the individual muscle bursts varied between 90 and 160 ms. However, the mean burst duration did not vary across movement conditions ($P>0.01$). This was the case for all subjects when movement timing was explicitly controlled and when it was not. This was also the case for the three subjects who repeated the experiment with the upper arm in a horizontal position. Thus the variation in agonist burst magnitude noted above was not due to an increase in burst duration, but presumably to an increase in the amplitude of the burst.



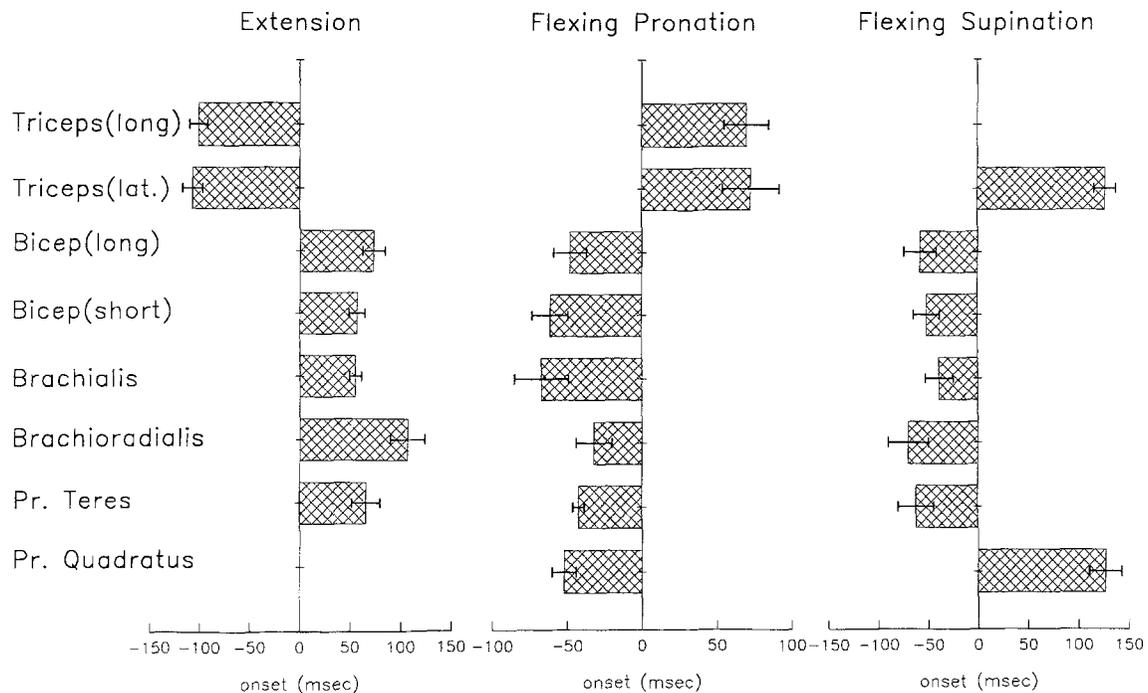


Fig. 10 Mean burst onset time relative to movement onset time across eight muscles for three different movements. Bars to the left of zero are agonists, bars to the right of zero are antagonists (absence of a column indicates no phasic activity for that muscle in a given movement condition). All muscles acting as agonists increase activity at approximately the same time. Muscles acting as antagonists show the same pattern. Error bars show standard deviations. Data shown are from subject 2

Discussion

The determinants of arm motion in multiple degrees of freedom were investigated by examining EMG activity associated with movements about the elbow in two degrees of freedom. Movements of varying amplitude were performed in each degree of freedom, both separately and together.

In multiarticular muscles, such as biceps brachii and pronator teres, agonist burst magnitudes observed in movement in two degrees of freedom did not, in general, differ from the sum of the magnitudes of the individual movements. The empirical summation of agonist burst magnitudes found in these trials suggests that the central

Fig. 9A–D Kinematic patterns and EMG activity for four different two-degree-of-freedom movements, from four different subjects, in which either biceps brachii or pronator teres act as agonist to motion in one degree of freedom and antagonist to motion in the other. **A** During an extending supination, biceps brachii displays burst activity along with triceps brachii (a pure agonist) and pronator teres (a pure antagonist). **B** During a flexing pronation, biceps brachii again shows agonist and antagonist components. **C** Pronator teres displays a large agonist burst concurrent with biceps and a smaller antagonist burst with pronator quadratus during a flexing supination. **D** The opposite pattern is seen in a trial involving an extending pronation. Pronator teres displays a small agonist burst (concurrent with triceps) and a larger antagonist burst (concurrent with biceps)

commands for motion in the component degrees of freedom may themselves be superimposed. When EMG burst magnitudes did not summate, the magnitude of the agonist burst in the combined movement was always greater than the sum of the agonist bursts in the component movements. Consistent with the findings of van Zuylen et al. (1988), this nonlinearity may reflect the presence of separate motor unit subpopulations: those whose recruitment thresholds depend on motion in single degrees of freedom, and others whose thresholds depend on motion in two degrees of freedom.

Multiarticular muscles often displayed agonist and antagonist activity in the same movement. This likewise suggests that, even when a muscle must perform opposing functions in a single movement, the control signals subserving the component movements may be superimposed. Since this behavior was not observed in every trial, other factors may limit the expression of both bursts within the same movement. One possibility is that their appearance is related to the movement amplitude or torque requirements for motion in each degree of freedom.

The idea that control signals for motion in individual degrees of freedom are superimposed implies that, at some level, they are planned separately. Indeed, a number of studies have suggested that reaching movements (which involve elbow flexion and extension) and rotation of the forearm may be planned independently (Lacquaniti and Soechting 1982; Perenin and Vighetto 1988; Soechting and Flanders 1993).

Previous work on isometric, two-degree-of-freedom elbow torques may provide insight into the nature of the mapping between control organized at the level of component movements and control signals at the level of commands to individual muscles. Under isometric conditions, van Zuylen et al. (1988) identified specific motor-

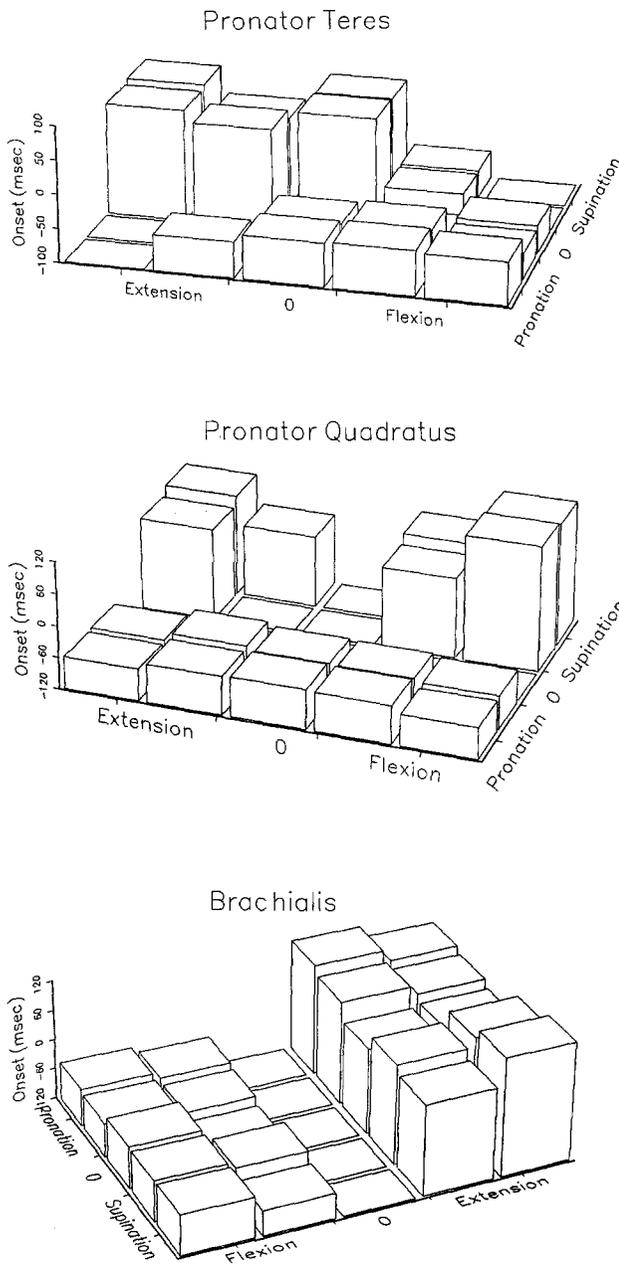


Fig. 11 Burst onset time relative to movement onset time for three muscles across all movement conditions. Each bar represents the mean of all trials within a single movement condition. *Taller bars* correspond to those movement conditions in which the muscle acts as antagonist, *shorter bars* correspond to the conditions in which the muscle acts as agonist. Absence of a bar indicates lack of phasic activity for that muscle. Data shown are from subject 3

unit subpopulations whose recruitment thresholds were dependent on torques in individual degrees of freedom or on torques in the two degrees of freedom combined. Thus, control at the level of individual degrees of freedom may be mapped onto control at the level of individual muscles using these subpopulations of motor units as a neuroanatomical substrate.

Previous studies examining shoulder-elbow movements in two degrees of freedom in the horizontal plane (Karst and Hasan 1991) and in the sagittal plane (Flan-

ders and Herrmann 1992; Flanders et al. 1994) have found that the timing of muscle activity varied for movements in different directions. In contrast, we have found that across all muscles tested the agonists all start firing together and the antagonists likewise come on together. In studies such as those reported by Karst and Hasan (1991) and Flanders and colleagues (Flanders and Herrmann 1992; Flanders et al. 1994), subjects typically produced point-to-point arm movements in which relatively straight line hand paths were observed. Asynchronies in the timing of joint motion and hence muscle activation are necessary to achieve such straight-line hand paths. In the present study subjects were not constrained to couple movements, as is observed in target-directed pointing. However, neither were subjects specifically constrained to produce simultaneous movement in two degrees of freedom at the elbow. It is interesting to observe that even in movements in the present study in which timing was not explicitly controlled, synchronous agonist and antagonist burst onsets were nevertheless obtained.

It has been noted that forearm rotation is uncoupled from elbow motion (Lacquaniti and Soechting 1982). That is, the torques produced by rotation of the forearm do not affect the torques produced during flexion and extension of the arm. In a system such as that involving shoulder and elbow, variable muscle burst onsets may help produce smooth movement in the face of inertial, Coriolis, and other interaction torques. In coordinating multiple muscle activity patterns in the present task, it may be unnecessary to stagger muscle onsets. Synchronous timing of muscle bursts seen in the present study may simply reflect this uncoupling.

Muscle burst durations were found to not vary over the different movement conditions. This indicates that phenomena such as the gradation of agonist burst magnitude with motion in a second degree of freedom primarily reflects changes in burst amplitude rather than burst duration. The relatively constant burst duration observed here is consistent with previous work on single-joint elbow movements within this range of amplitudes (Brown and Cooke 1984) and on double-joint movements where movement time was held constant over different movement amplitudes (Buneo et al. 1994).

To summarize, we have examined EMG correlates of motion in two degrees of freedom about the elbow. We found that muscles fall into two categories with respect to agonist burst magnitude: those whose burst magnitude varies with motion in a second degree of freedom in a graded fashion and those whose burst magnitude does not. We also observed that during movements in which multiarticular muscles act as agonist to motion in one degree of freedom and antagonist in the other, the muscle activity often has both agonist and antagonistic components. Together these findings suggest that central commands for motion in individual degrees of freedom may be superimposed in producing movements in two degrees of freedom. Because these behaviors were not always observed, factors leading to variability in these patterns require further study.

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