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Short-term synchronization of motor units in human extensor digitorum communis muscle: relation to contractile properties and voluntary control

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Abstract. Synchronous activity was studied in relation to the contractile properties of pairs of motor units (MUs) recorded with independent microelectrodes in the right *extensor digitorum communis* muscle (EDC) of human subjects during isometric finger extension. MU contractile properties were characterized in terms of the rise time and amplitude of twitch tensions extracted by spike-triggered averages of the extension force. Synchronization of MU discharges appeared in the form of narrow central peaks in the cross-correlograms of 35 of 50 pairs of MUs, suggesting the contribution of common last-order neurons. Synchronization peaks tended to be briefer and higher among pairs of MUs with slower and smaller twitches than among pairs of MUs with faster and larger twitches. The higher peaks of slow-contracting MUs suggest a greater effectiveness of the common synaptic inputs. The broader peaks of fast-contracting MUs might reflect an additional synchronization of the inputs to fast MUs at high force levels. The areas of the cross-correlogram peaks were similar for both groups and suggest that under our conditions, about three motoneurons would discharge synchronously for a given motoneuron spike. To test whether the amount of MU synchronization could be altered voluntarily, four subjects attempted to increase or decrease synchrony, using as feedback clicks triggered by coincident firings of the recorded MUs. In nine of 15 conditioning sessions, the magnitudes of the synchronization peaks showed significant changes in the intended direction. These results imply that supraspinal centers can control the relative amount of inputs that contribute to the synchronization of motoneuron discharges during voluntary contraction of EDC.

Key words: Motor unit – Twitch tension – Short-term synchronization – Human

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Introduction

During muscle contraction, a pair of motoneurons may be activated by two distinguishable sources of synaptic drive: they may receive common synaptic input from cells that send divergent connections to both motoneurons, or they may receive simultaneous drive from separate cells that are coactivated. The relative amount of common synaptic input versus simultaneous drive can be assessed by cross-correlating the activity of the motoneurons or, equivalently, the activity of the corresponding motor units (MUs). Sources of common synaptic input would produce nearly simultaneous arrival of excitatory postsynaptic potentials (EPSPs) in their target motoneurons, generating a narrow peak around the origin of the cross-correlogram of the MU discharges – the so-called short-term synchronization peak (Sears and Stagg 1976; Kirkwood 1979; Kirkwood and Sears 1991). Independent sources of simultaneous input would not generate such a narrow peak, although they could produce a broad peak if the sources are synchronized by common inputs (Kirkwood et al. 1982) or phasically coactivated.

In human subjects, short-term synchronization of MUs has been documented during voluntary contraction in single muscles of the hand, forearm, leg, chest and jaw (Buchthal and Madsen 1950; Milner-Brown et al. 1975; Dietz et al. 1976; Dengler et al. 1984; Datta et al. 1986, 1991; Adams et al. 1989; Datta and Stephens 1990; Nordstrom et al. 1990,1992; Bremner et al. 1991a,b; Davey et al. 1990). However, the origin of the underlying common inputs remains to be determined.

Common synaptic inputs to motoneurons may derive from several sources, including last-order spinal interneurons. Other likely sources include the Ia afferent fibers and the supraspinal premotoneuronal cells with descending fibers that contact multiple motoneurons. In cats, Ia afferent fibers have been shown to contact virtually all the homonymous motoneurons of hindlimb muscles (Mendell and Henneman 1971), and in primates, single afferents facilitate many target muscles (Flament et al. 1992). Recent studies suggest that single corticomotoneu-

ronal cells may facilitate up to 75% of the MUs in their target muscles (Mantel and Lemon 1987; Fortier et al. 1989). Several clinical observations favor the contribution of supraspinal centers in the synchronization of MU discharges during voluntary contraction: MU synchronization is still present in deafferented patients (Buchthal and Madsen 1950; Datta et al. 1991) and is less frequent or markedly altered in patients with spinal lesions and cortical strokes (Davey et al. 1990; Datta et al. 1991).

To date, there is little documentation of the distribution and the strength of the common inputs that contribute to activation of different classes of motoneurons during voluntary contraction. The effectiveness of common inputs in synchronizing the discharge of their target neurons can be expected to depend on the characteristics of their EPSPs. In anesthetized cats, the smallest motoneurons receive the largest EPSPs from several sources, such as Ia afferents, compared with larger motoneurons (see Munson 1989 for review). To the extent that these trends apply to the common inputs active during voluntary contraction of the extensor digitorum communis (EDC) in humans, one may expect that the slow-contracting MUs corresponding to the small motoneurons with the lowest recruitment threshold would exhibit stronger short-term synchronization. However, this hypothesis was not confirmed in a study in which MUs were differentiated on the basis of the force level at which they fire tonically (Datta and Stephens 1990). These authors reported that "the strongest synchronization was most frequently observed between pairs of units where both units were of high recruitment threshold," which should correspond to larger motoneurons. This unexpected result deserved further investigation. Therefore, the first aim of our study was to compare the amount of synchronization of MUs differentiated on the basis of their contractile properties, using spike-triggered averages of force to extract the twitch tension of a single MU during voluntary contraction (Milner-Brown et al. 1973a).

The second aim of our study was to determine whether synchronous activity of MUs could be voluntarily controlled. Changes in MU synchronization have been reported under various physiological conditions, including fatigue (Buchthal and Madsen 1950; Lippold et al. 1957), tremor (Dietz et al. 1976), and certain types of motor dysfunction (Buchthal and Madsen 1950; Dengler et al. 1986; Davey et al. 1990; Datta et al. 1991; Baker et al. 1992). MU synchronization was shown to be stronger during voluntary muscle activation than during reflex activation (Adams et al. 1989). MU synchronization was also enhanced after daily exercise involving brief periods of maximal muscular contraction (Milner-Brown et al. 1975). Such variations in MU synchronization suggest that the relative effectiveness of the common inputs may be modulated, depending on physiological or behavioral conditions. To investigate whether the relative proportion of common input to MUs could be rapidly altered by descending commands, we tested the ability of human subjects to increase or decrease voluntarily the synchronous discharges of the recorded MUs using auditory feedback.

Materials and methods

Recording procedures

Data were obtained from five right-handed subjects (two females, three males) who gave their informed consent and could withdraw from the experiment at any time. The study was approved by the University of Washington Human Subjects Review Committee. Each subject sat with the right arm semi-prone and the fingers extended against a force transducer. The backs of the middle phalanges of digits 2 to 5 were placed against a vertical rod attached to a strain-gauge bridge that transduced the torque generated by the extension of the fingers. Force output was amplified and recorded as DC force (0–5 kHz) and AC force (band-pass filtered at 0.1–1 kHz). The static DC force was calibrated by applying a spring at various force levels to the point of finger contact: the dynamic (step) response of the force transducer was calibrated by rapidly releasing the spring. The AC force was used to extract spike-triggered averages of the twitch tension associated with MU action potentials (Milner-Brown et al. 1973a).

Independent MU recordings were obtained via two or more varnish-insulated tungsten microelectrodes inserted transcutaneously into the EDC of the right arm: the microelectrodes were separated by 2–3 mm transversely and up to 2 cm longitudinally. A surface electromyographic electrode provided a common indifferent electrode. Acceptance pulses were generated for each MU by passing the microelectrode signal through a time-amplitude window discriminator.

Biofeedback conditioning

To help control activity of the studied MUs, subjects observed the expanded action potentials on an oscilloscope screen and received auditory feedback of the discriminated action potentials. During the initial part of recording used for spike-triggered averaging of the twitch tension, the firing rate of each MU was kept as low as possible (usually < 8 imp/s). Then subjects made the two MUs fire regularly and continuously for 5–15 min to provide spike trains for the cross-correlation analysis. For the synchrony or desynchrony conditioning sessions in which the subjects attempted to change the amount of short-term synchrony between the recorded MUs, feedback was provided by clicks generated whenever the action potentials of the two MUs occurred within 5 ms of each other.

After 2–3 min of recording without synchrony feedback (preconditioning control period), the synchrony feedback was turned on and the subjects were asked to increase the frequency of the synchrony clicks for 3–10 min (synchrony conditioning period). Whenever possible, this was followed by a third period of recording during which the subjects were asked to reduce the frequency of the synchrony clicks (desynchrony conditioning period).

Data analysis

The DC and AC force, the single MU recordings, and the corresponding acceptance pulses were stored on analog tape for off-line analysis with a PDP 11/73 computer. A measure of the apparent twitch tension of each MU was obtained from spike-triggered averages of the AC force signal, using the MU acceptance pulses as triggers. As illustrated in Fig. 1**A**, the spike-triggered averages included (1) the average AC force, which provides measures of the rise time and the amplitude of the twitch, (2) the waveform of the triggering action potential from the analog recording signal, and (3) the autocorrelogram of the trigger MU discharge, which confirmed the quality of the isolation of the triggering MU. The DC force signal (not shown) was averaged simultaneously to document the average force level at which the MU fired tonically.

A cross-correlation histogram of the activity of each pair of MUs was computed using the acceptance pulses generated by the

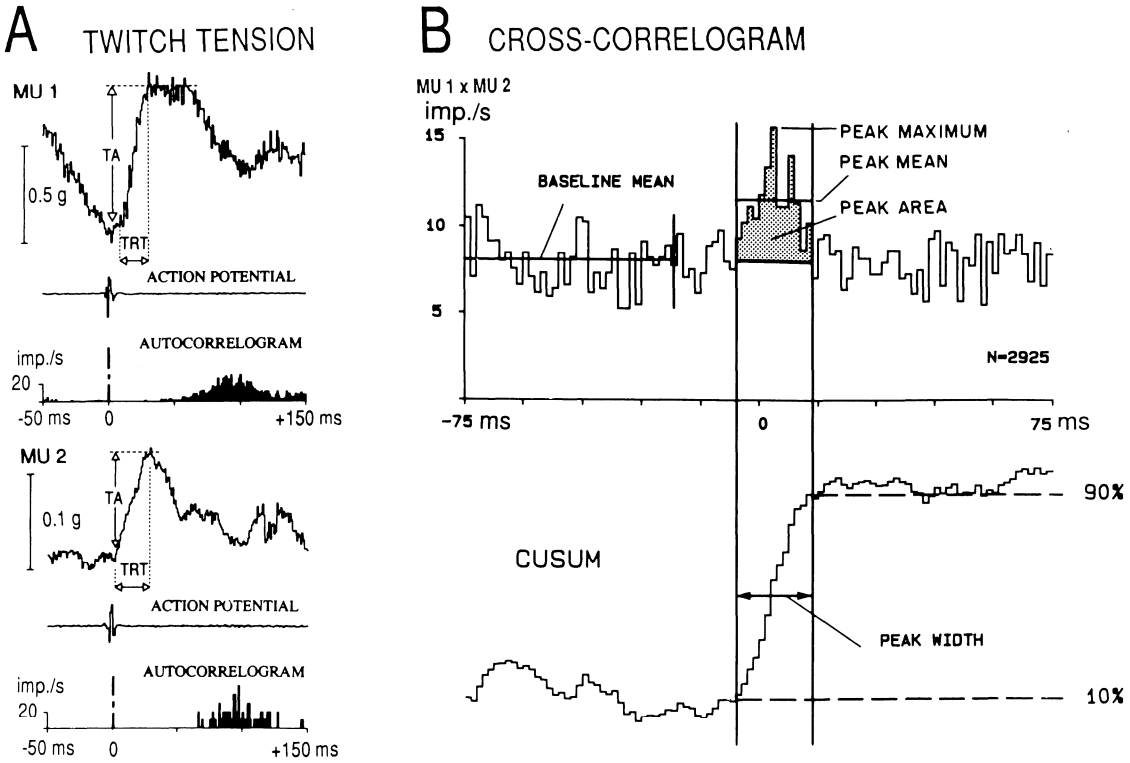

Fig. 1. A Twitch tension of two MUs recorded simultaneously. The AC force signal (*top traces*), the analog signal of the trigger MU action potential (*middle*), and the autocorrelogram of the acceptance pulses (*bottom*) were averaged for 800 sweeps (MU 1) and 100 sweeps (MU 2). **B** *Top*: Cross-correlation histogram of the discharges of MU 1 (trigger) and MU 2 (target). Bin counts are converted to impulses per second (imp/s) = counts per bin /(binwidth × number of sweeps). *Bottom*: CUSUM of the histogram relative to the mean baseline count (over the first 35 bins of the cross-correlogram). *Vertical lines* mark levels of 10% and 90% in the rise of the CUSUM, used to delimit the peak in the cross-correlogram

MU spikes. The reference or "trigger" MU pulses triggered an averaging program that computed the times at which the associated "target" MU discharged within a 150 ms interval centered on the reference pulse, with binwidths of 1.5 ms. These averages also included the autocorrelogram of the reference pulses and the analog signals from both microelectrodes. The bin counts of the cross-correlograms were converted to firing rate (imp/s). The features of the cross-correlograms were identified and measured as illustrated in Fig. 1**B**. The baseline period comprised the first 52.5 ms of the cross-correlogram. A cumulative sum (CUSUM) was computed by adding the successive differences between each bin content and the baseline mean (Ellaway 1978). Correlogram peaks were identified as a sustained rise in the CUSUM. The onset and offset of the peak were defined as the first bins that exceeded the 10% and 90% levels of the CUSUM rise, respectively, and their difference determined the peak width. The significance of the correlogram peak was assessed by calculating the z score, which determines by how many standard deviations the mean counts in the peak exceeded the mean counts in the baseline (Cox and Lewis 1966; Garnett and Stephens 1980). The critical value for the significance of the peak was set at $P < 0.005$ with $z > 2.8$.

The magnitude of the significant peaks was quantified in terms of five parameters. Three parameters measured the relative peak height, namely, the mean percent increase (MPI) above baseline (Cope et al. 1987) and the parameters k (Sears and Stagg 1976) and k' (Ellaway and Murthy 1985). Two parameters measured the peak area above baseline, normalized either to the number of triggers (Cope et al. 1987) or to time, corresponding to the so-called "common input strength", or CIS (Nordstrom et al. 1992), where:

MPI = 100 × [peak mean - baseline mean]/baseline mean

k = peak maximum/baseline mean

k' = peak mean/baseline mean

area = peak counts above the baseline mean/number of triggers

CIS = peak counts above the baseline mean/duration of recording

For every pair of MUs, two cross-correlograms were computed, using each MU as trigger. MUs were considered as synchronized when significant peaks ($z > 2.8$) were present in both cross-correlograms. The mean of the two values of each peak parameter (width, k, k', MPI, area, CIS) was calculated for every pair.

To determine whether the subject's attempts to control the synchronous firing were successful in changing the central features in the cross-correlograms, we computed a difference histogram by subtracting the cross-correlogram computed for the control period (before conditioning) from the cross-correlogram computed for the synchrony conditioning period. The presence of a central peak or trough in the difference histogram was taken as evidence that the synchrony conditioning produced a selective increase or decrease of MU synchronization in that region. A t-test was used to assess the significance of the change in the bin contents in this region of the difference histogram with respect to the bin contents of the baseline. In a few cases, a modified t-test (t^*) (Snedecor and Cochran 1980) was used whenever the variance in the peak differed significantly from the variance in the baseline.

Results

Eighty-five MUs were recorded in the EDC muscle of five subjects. Most MUs were optimally activated by the extension of a single digit (digit 2, $n = 2$; digit 3, $n = 31$;

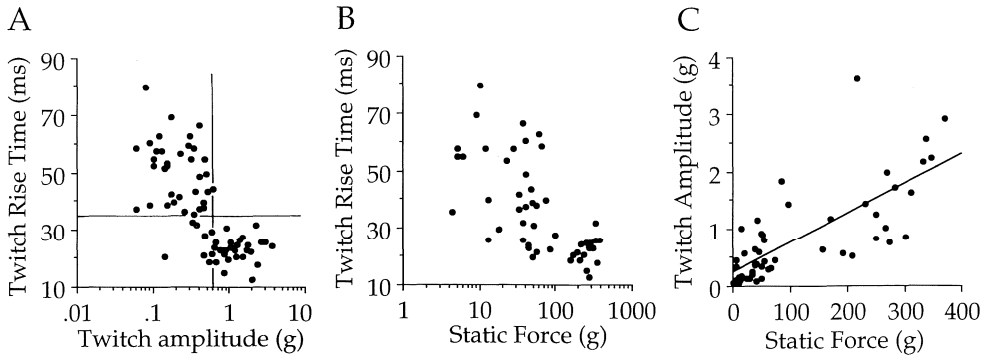

Fig. 2A–C. Relation between mechanical parameters of MU twitch tensions for 78 MUs. **A** Relation between twitch rise time (TRT) and twitch amplitude (TA) on a semilog plot. **B** TRT plotted against mean static force during averaging. **C** TA against static force ($r = 0.47$, $p = 0.01$)

digit 4, $n = 22$; digit 5, $n = 4$). Single MU discharges were recorded for 5–15 min with no apparent fatigue; firing rates ranged from 2.4 to 16 imp/s and static force ranged from 0.8 to 484 *g*.

Contractile properties

A twitch tension was determined for 79 of the 85 recorded MUs from the spike-triggered averages of the AC force compiled during periods when the subjects kept the firing rates as low as possible (usually below 8 spikes/s). The average twitch tensions of two MUs (MU1 and MU2) are shown in Fig. 1**A**. The twitch rise time (TRT) was measured from the onset of the rise in the force average to its peak (MU1 TRT = 22 ms, MU2 TRT = 35 ms). The TRTs of the whole population ranged from 13 to 70 ms. The twitch amplitude (TA) was measured from the onset to the peak of the force rise (MU1 TA = 0.92 *g*, MU2 TA = 0.14 *g*). The amplitudes of the measurable twitches ranged from 0.06 to 3.65 *g*.

As could be expected, the twitches with the fastest rise times tended to have the largest amplitudes. As illustrated in Fig. 2**A**, there was a significant inverse relation between the TRTs and TAs. Most units fell into one of two quadrants delineated by the dividing lines at 35 ms TRT and 0.5 *g* TA.

The absolute recruitment threshold of the MUs could not be determined reliably because the net extension force included possible contributions of synergistic muscles. Nevertheless, the MUs recorded at lower average DC static forces during the twitch averaging tended to have longer twitch contraction times (Fig. 2**B**) and smaller twitch amplitudes (Fig. 2**C**). Very similar relations were found for the MUs ($n = 35$) recorded in a single subject.

These results suggest the presence of two groups of MUs: one group consisted of relatively slow-contracting MUs (TRTs $\geq$ 40 ms), which produced the smallest twitch tensions (TA $<$ 0.5 *g*) and were most often recorded with static force below 100 g; the second group consisted of relatively fast-contracting MUs (TRTs $\leq$ 30 ms), which produced the largest twitch tensions (TA $>$ 0.5 *g*) and were most often recorded with static force higher than 100 *g*.

Synchronization characteristics

The correlation between MU discharges was studied for 50 pairs of tonically firing MUs. The representative cross-correlation histogram in Fig. 1**B** shows the discharge of a small twitch unit, MU2 (Fig. 1**A**, bottom), in relation to the action potentials of a large twitch unit, MU1 (Fig. 1**A**, top). The MUs fired with mean frequencies of 15.2 and 7.5 imp/s, respectively, and both were activated by extension of digit 3. The peak of the cross-correlogram had an offset of 4.5 ms relative to the origin of the histogram, indicating a tendency for MU2 to fire in synchrony with MU1 after a slight delay. This delay could be due to a longer conduction time from the spinal cord to the muscle fibers for MU2.

Statistically significant peaks ($P < 0.005$, z values > 2.8) appeared in both cross-correlation histograms computed for 35 of 50 pairs of MUs, revealing a substantial amount of synchronous firing among most EDC MUs. The widths of these peaks ranged from 3 to 16 ms (mean 9.3 $\pm$ 3.4 ms SD). The mean height of the peaks relative to the baseline, as measured by k', ranged from 1.2 to 3.49 (mean 1.7 $\pm$ 0.45): this corresponds to a MPI above baseline of 20–249%. The maximum peak counts had k values of 1.4–4.25 (mean 2.21 $\pm$ 0.60). The areas of the peaks, representing the number of above-chance coincidences per trigger, ranged from 0.014 to 0.080 spikes per trigger (mean 0.045 $\pm$ 0.017). The CIS values, representing the number of above-chance coincidences per second, ranged from 0.093 to 1.052 per second (mean 0.400 $\pm$ 0.241).

The relative height of the correlogram peak, as measured by k' and k, was inversely related to the geometric mean discharge frequency of cross-correlated MUs ($r = -0.34$, $P = 0.03$ for k' and $r = -0.28$, $P = 0.11$ for k), as previously reported for gamma motoneurons (Ellaway and Murthy 1985) and alpha motoneurons (Nordstrom et al. 1992). This suggests that MUs with the slowest firing rates might exhibit the highest levels of synchronization. Nevertheless, the mean discharge frequencies of the pairs that had significant cross-correlogram peaks (8.0 $\pm$ 2.7 imp/s) did not differ significantly from rates of the unsynchronized pairs (7.6 $\pm$ 2.38 imp/s).

Synchronization of MU s related to extension of same or different fingers

Pairs of MUs related to extension of the same or different fingers did not differ significantly with respect to firing rate or contractile properties (geometric mean firing rate 8.2 ± 2.9 and 8.1 ± 2.3; mean TRT 43.2 ± 15.2 and 38.3 ± 12.8 ms; mean TA 0.54 ± 0.67 and 0.63 ± 0.65 *g* for same and different finger pairs, respectively). Significant cross-correlogram peaks were found for 15 of 18 pairs of MUs activated by extension of the same fingers. In contrast, only 15 of 27 pairs activated by extension of different fingers exhibited synchronization peaks. This difference in incidence was significant according to the contingency table ($\chi^2 = 3.75$, $P = 0.05$). However, the parameters of the correlogram peaks did not differ significantly for pairs controlling same or different fingers (peak width 8.5 ± 3.2 vs. 8.8 ± 4.8 ms; peak area 0.053 ± 0.023 vs 0.045 ± 0.019; CIS 0.435 ± 0.269 vs. 0.356 ± 0.200; k' 1.81 ± 0.30 vs. 1.83 ± 0.49; k 2.14 ± 0.48 vs 2.26 ± 0.53).

MU synchronization and contractile properties

To determine whether particular types of MUs were synchronized preferentially, we compared the contractile properties of pairs that had significant cross-correlogram peaks with those of unsynchronized pairs. Each pair was characterized mechanically by the mean values of the TRTs and TAs of its constituent MUs. No significant difference was found between the mean TAs (synchronized 0.57 ± 0.69 *g*; unsynchronized 0.63 ± 0.58 *g*) nor between the mean TRTs (synchronized 40.44 ± 13.40 ms; unsynchronized 35.77 ± 13.96 ms). This result indicates that synchronization, as measured by the presence of cross-correlogram peaks, did not preferentially affect one category of MUs.

We next determined whether the parameters of the cross-correlogram peaks were related to the contractile properties of the MU pairs. Figure 3 illustrates the peak width, the relative peak height k', peak area, and the CIS plotted against the mean TRT (Fig. 3, left) and the mean TA of each pair (Fig. 3, right). Pairs related to same or different fingers are represented respectively by white or black circles. For purposes of comparison, regression lines are fitted to the data.

The width of the cross-correlogram peaks was negatively correlated with the mean TRT (Fig. 3**A**, $r = -0.58$, $P = 0.0001$) and positively correlated with the mean TA (Fig. 3**D**, $r = 0.54$, $P = 0.003$). A positive correlation ($r = 0.43$, $P = 0.03$), not illustrated, was also observed between the peak width and the mean static force at which each pair was recorded.

The relative peak height k', peak area, and the CIS all tended to be positively correlated with the mean TRT (Fig. 3**B-D**). A similar trend, not illustrated, was found for the correlation between k and the mean TRT ($r = 0.29$, $P = 0.096$). The reverse trend was found between these parameters (k, k', area, and CIS) and the mean TAs, but this was much weaker and did not reach significance (Fig. 3**F-H**).

The regression analysis performed separately for the pairs of MUs related to either same finger (Fig. 3, white circles) or different fingers (Fig. 3, black circles) showed comparable trends between the mean TRT and all of the peak parameters: the regression coefficients for each subset were close to those calculated for the whole population, but did not reach the $P = 0.05$ level of significance.

Altogether, these results suggest that the pairs with the longest mean TRTs tended to exhibit the largest amount of synchronization and the narrowest peaks. In contrast, the synchronization of the pairs with the shortest mean TRTs tended to be weaker and less tightly coupled, as suggested by their broader peaks and smaller k, k', CIS and area values.

To further analyze the relation between synchronization parameters and MU contractile properties, we compared the correlogram peaks of pairs in which both MUs could be considered to be "slow" or "fast" on the basis of their TRTs and TAs. In the group of slow pairs, both MUs had TRTs longer than 40 ms and produced TAs smaller than 0.5 *g*. In the group of fast pairs, both MUs had TRTs shorter than 30 ms and produced TAs larger than 0.5 *g*. The relative incidences of the significant peaks within the slow and fast groups (15/20 and 9/14) did not differ significantly. The synchronization characteristics of the fast and slow pairs are summarized in Table 1. In general, the significant differences assessed by the analysis of variance (marked by asterisk) indicated that slow

Table 1. Synchronization measures for pairs of motor units that were both "slow" or both "fast"

	Proportion of pairs with significant correlogram peaks	Firing rate (imp/s)	Peak width (ms)	Peak area	CIS	k′
"Slow" group (TRT ≥ 40 ms, TA < 0.5 *g*)	15/20	7.9 ± 2.9 (3.5–13.5)	7.2 ± 2.1 * (3.0–10.5)	0.048 ± 0.020 (0.018–0.074)	0.419 ± 0.284 (0.105–1.124)	1.83 ± 0.32 ** (1.45–2.45)
"Fast" group (TRT ≤ 30 ms, TA > 0.5 g)	9/14	7.1 ± 1.7 (4.5–9.5)	12.4 ± 2.7 (7.5–15.0)	0.047 ± 0.012 (0.031–0.067)	0.340 ± 0.165 (0.137–0.653)	1.53 ± 0.13 (1.38–1.72)

Upper line gives mean ± standard deviation, lower line gives range
* $P = 0.001$; ** $P = 0.04$

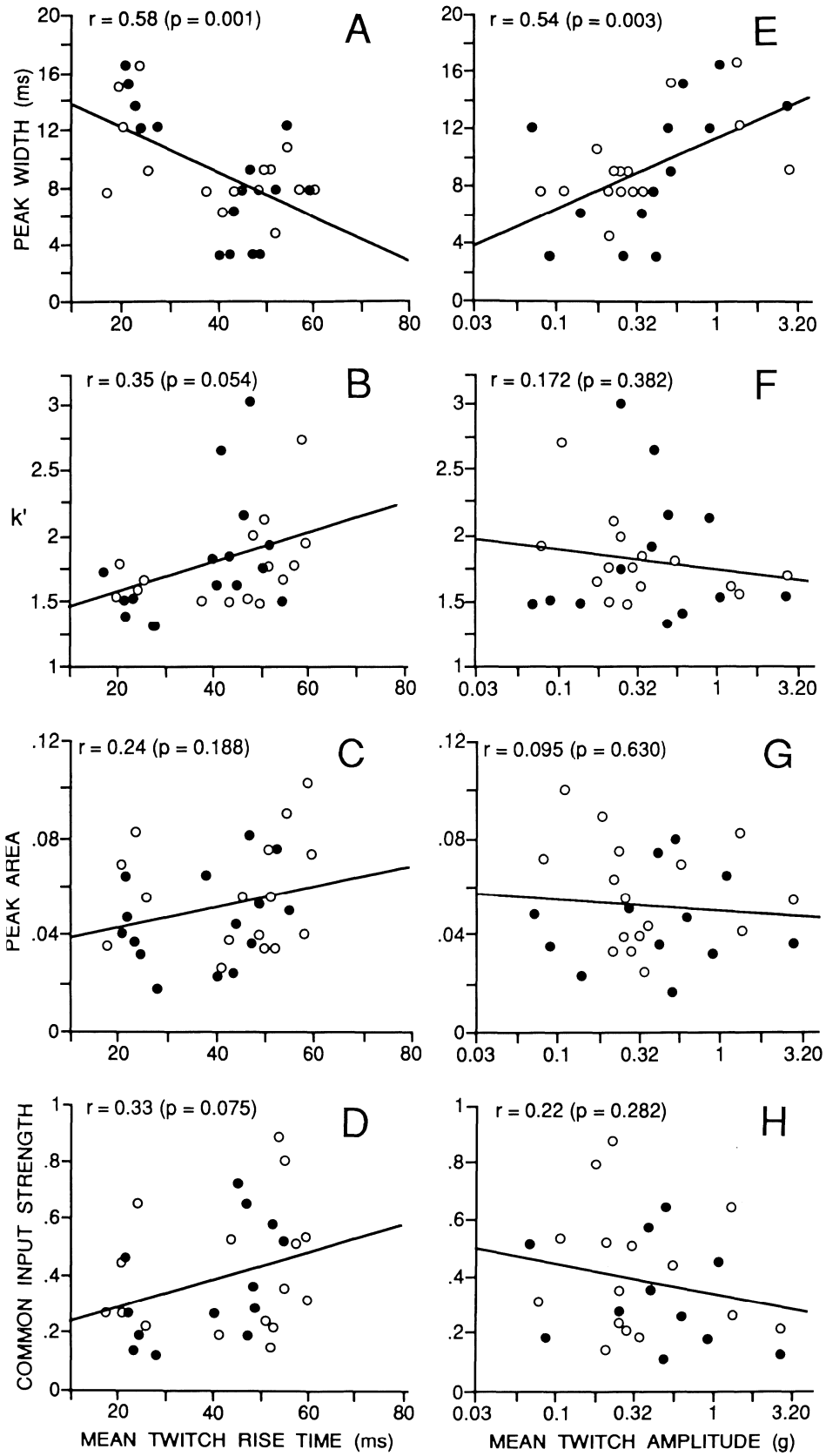

Fig. 3A–H. Relation between parameters of cross-correlogram peak and mean twitch parameters of MU pairs related to same finger (○) and different fingers (●). Correlogram parameters from top to bottom are peak width (ms), relative peak height k', peak area, and CIS. These are plotted against TRT (*left column*) and TA (*right column*)

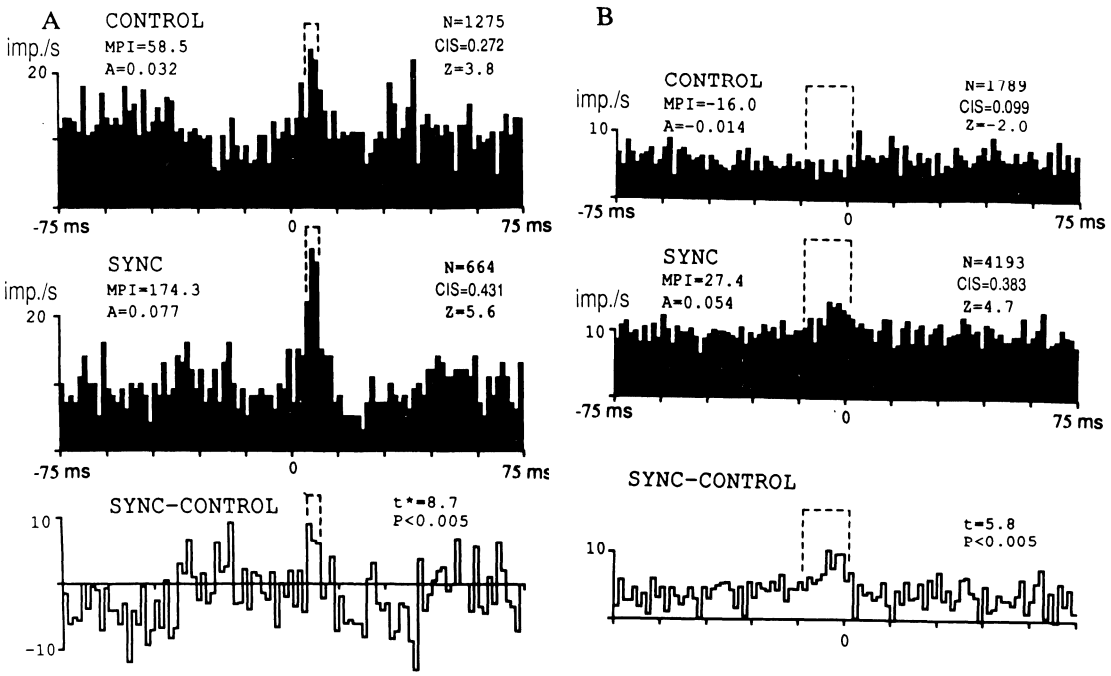

Fig. 4A,B. Changes in correlograms with synchrony conditioning. **A** Cross-correlograms computed for two MUs in subject A. The trigger and target MUs discharged at 12.3 and 8.5 imp/s in the control period (*CONTROL*) and at 12.5 and 5.6 imp/s in the synchrony conditioning period (*SYNC*). The difference between the two correlograms (*SYNC − CONTROL*) shows an increase in the counts over an interval (- - -) corresponding to the 10–90% rise in the CUSUM of the SYNC cross-correlogram. The significance of this increase is assessed by the *t*-test comparing the means of the bin counts in the dashed interval and in the baseline (first 35 bins of the difference trace). **B** Cross-correlograms computed for two MUs recorded in subject B with firing rates of 7 and 5.6 imp/s in the control period and 7.1 and 9.4 imp/s in the synchrony conditioning period. A peak appeared *de novo* in the SYNC histogram (- - -), resulting in a highly significant increase in the counts over this interval in the difference trace (bottom). *N*, number of averaged sweeps; *z*, number of standard deviations by which the peak mean exceeded the baseline mean; *MPI*, mean percent increase of counts in the peak region; *A*, area of the peak; *CIS*, common input strength; t^* = modified *t*-test used when the variance in the baseline differs significantly from the variance in the peak (Fisher test); p = probability level for statistical significance

pairs tended to have narrower and higher cross-correlogram peaks than fast pairs.

An analysis of variance was performed between the four subgroups of MUs represented by slow and fast pairs related to the same or different fingers. The differences in peak height k' did not reach the level of significance ($F_{3,20} = 2.27$) among the four subgroups, but k' values were significantly larger for the slow pairs (related to same or different fingers) than for the fast pairs ($F_{1,20} = 4.74$, $P < 0.05$); k' was not different for pairs related to the same finger (slow and fast) versus pairs related to different fingers ($F_{1,20} = 0.47$). The differences in peak width were highly significant among the four groups ($F_{3,20} = 18.65$, $P < 0.0001$), and were significant only for fast pairs versus slow pairs ($F_{3,20} = 52.18$, $P < 0.0001$) but not for pairs related to the same finger versus pairs related to different fingers ($F_{1,20} = 0.73$). The differences observed for the other parameters – k, area and CIS – between the fast and slow pairs (related to same or different fingers) did not reach significance in this analysis.

Only four MU pairs could be considered mixed, i.e., including one fast- and one slow-contracting MU according to the above criteria. Two of these four pairs exhibited significant cross-correlogram peaks, but this sample was too small to allow a quantitative comparison with slow or fast pairs.

Twelve pairs could not be type-identified, either because no consistent twitch had been extracted by spike-triggered averaging, or because the twitch rise time or amplitude did not meet the criteria used to differentiate fast and slow MUs. Among this group, eight pairs presented significant peaks (mean peak width 7.3 ± 0.4; peak area 0.043 ± 0.017; CIS 0.454 ± 0.281; k' 1.73 ± 0.27; k 1.89 ± 0.31).

Voluntary control of short-term synchronization

Four subjects attempted to change voluntarily the degree of synchronous firing of 12 pairs of MUs in a total of 15 sessions of synchrony and desynchrony conditioning. Increases in the amplitude of the correlogram peak or the appearance of a significant peak were observed in eight of the 11 sessions of synchrony conditioning, in which the subject attempted to increase the frequency of the synchrony feedback. Conversely, decreases in the amplitude of cross-correlogram peaks were observed in the four desynchrony conditioning sessions, in which the subject was asked to reduce the frequency of the synchrony feedback.

Increases in the peak amplitude were observed during the synchrony conditioning of three slow-contracting MU pairs, two fast-contracting MU pairs, two mixed

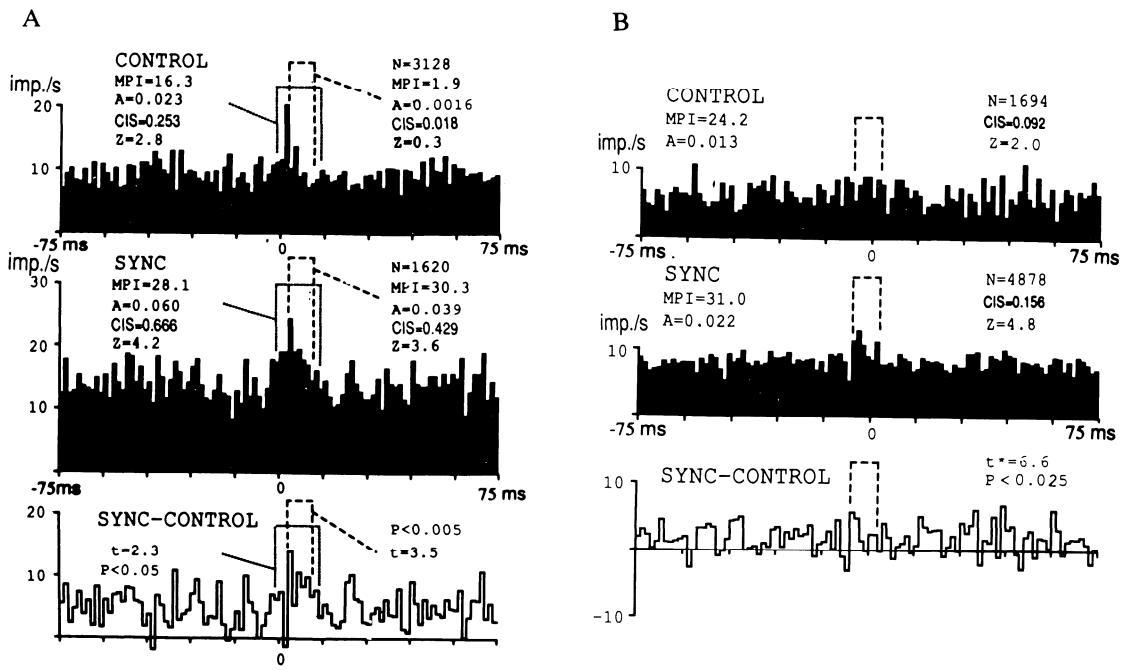

Fig. 5. **A** Cross-correlograms computed for two MUs recorded in subject A for the control period and the synchrony conditioning period. The difference trace shows a narrow (- - -) and broad (——) peak interval. Statistics for both intervals are shown above the histograms. **B** Cross-correlograms computed for two MUs recorded in subject C, with firing rates of 7.1 and 6.1 imp/s in the control period and 7.9 and 7.1 imp/s in the synchrony conditioning period. A peak appeared in the SYNC correlogram (- - -), but significance was not reached in the difference trace. Abbreviations as in Fig. 4

pairs, and one unidentified pair. Two of these pairs were related to the same finger and six were related to different fingers. The changes in the peak amplitude were not associated with consistent changes in the peak width; the peaks that appeared *de novo* for two pairs were rather narrow (4.5 and 7.5 ms).

Figure 4 illustrates successful attempts by subjects A and B to increase the degree of MU synchronization with the help of synchrony feedback. The MU pair in Fig. 4**A** included two slow MUs related to different fingers. This pair showed a short-term synchrony peak in the control period (top), which was clearly enhanced in the synchrony period (middle trace) over the same interval (dashed lines). The MPI almost tripled, probably due in part to the decrease in baseline firing rate. The peak area more than doubled, going from 0.032 synchronous spikes in the control period to 0.077 in the synchrony period, and the CIS increased from 0.272 to 0.431 synchronous spikes per second.

The fast pair illustrated in Fig. 4**B** was also related to different fingers. This pair developed a peak in the synchronization cross-correlation histogram (middle) over an interval (dashed lines) where no peak appeared in the control cross-correlogram (top). In this interval, the MPI, area, and CIS changed from negative to positive values. In these two examples, the specificity of the changes in the peak region was assessed by the highly significant values of the t (t^*)-test performed to compare the counts of the peak and the baseline regions in the difference histogram (Fig. 4**A, B**, bottom).

In some sessions, the CUSUM of the difference histogram suggested two intervals of increased synchrony, and statistics were calculated for both, as illustrated in Fig. 5**A** for a "slow" pair related to finger 3. Over the narrower peak interval in Fig. 5**A** (dashed lines), the difference between the control and synchrony periods was statistically significant: the control histogram showed no significant peak over this interval, which, during the synchrony period, exhibited a significant peak with an MPI of 30.3%, an area of 0.039, and a CIS of 0.429. The same trend was shown for a wider interval (continuous lines), which encompassed a broader peak in the synchrony histogram, whose area was almost three times that of the control interval. However, this increase did not reach the required level of significance in the difference histogram.

In one of the 11 synchrony conditioning sessions no change was observed during the synchrony period, and in five other sessions the apparent increases in synchronization did not reach statistical significance in the difference histogram. Four of these six sessions, deemed unsuccessful, represented the subjects' first exposure to the feedback task. An example of non-significant increase is illustrated in Fig. 5**B** for a fast pair related to different fingers. For this pair, a small but significant peak ($z = 4.8$) appeared in the cross-correlogram of the synchrony period over an interval that showed no significant peak in the control cross-correlogram. However, the t-test in the difference histogram failed to show statistical significance.

Figure 6 summarizes the changes in firing rates (**A**), peak area (**B**), and CIS (**C**) between the control and the synchrony conditioning sessions for the pairs with significant increases assessed by the difference histogram test (top) and for the pairs without such a significant increase (bottom). As shown in Figure 6**A** (top), the significant

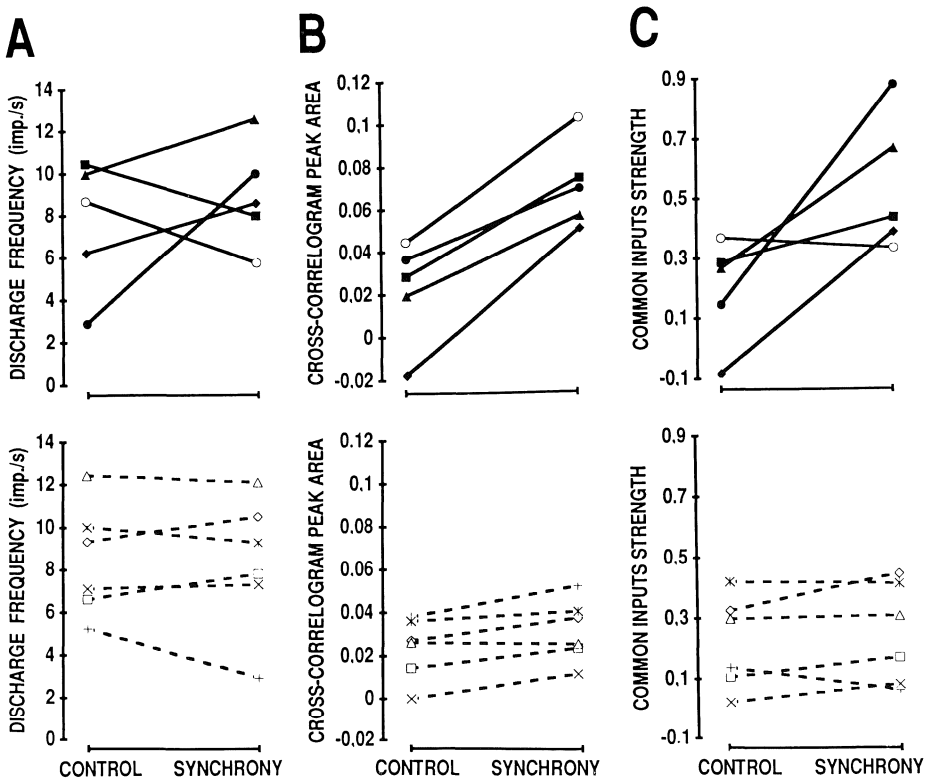

Fig. 6. Values of the geometric mean firing rate (**A**), the peak area (**B**), and CIS (**C**) in successive control and synchrony conditioning periods are plotted and joined by a line for each of the five pairs that presented a significant increase in the difference histograms (*top*) and for each of the six pairs that did not (*bottom*). Each symbol identifies one pair. The significant changes detected in the difference histograms were associated with an increase in CIS for all pairs (*top, black symbols*) but one

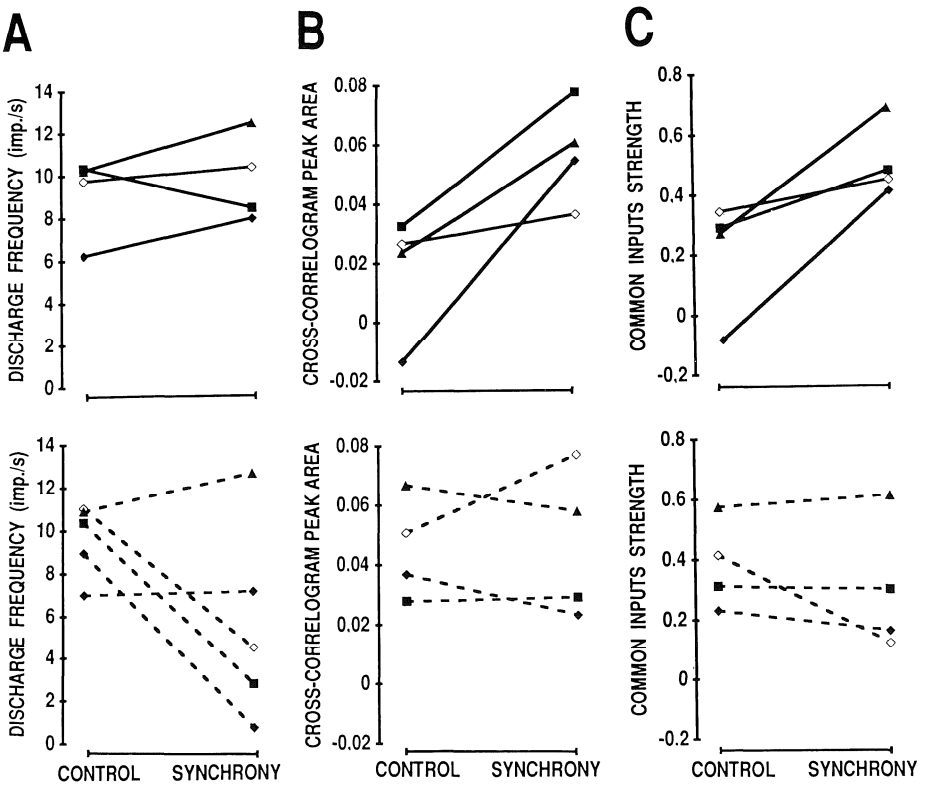

Fig. 7. Values of the geometric mean firing rate (**A**), the peak area (**B**), and the CIS (**C**) in the successive control and synchrony conditioning periods are plotted and joined by a line for four conditioned pairs (*top*) and five unconditioned pairs recorded simultaneously (*bottom*). The same symbol is used for pairs recorded simultaneously. Note the lack of increase in area and CIS for the three unconditioned pairs recorded concurrently with three successfully conditioned pairs (*black symbols*)

increases in synchronization could occur in association with either an increase or a decrease of the geometric mean of the MU firing rates. The peak area increased for all pairs (Fig. 6**B**, top) and CIS increased for all but one of the pairs (Fig. 6**C**, top). The pair whose CIS did not increase (despite an increase in area) had a much lower discharge frequency for one MU during the synchrony conditioning period (Fig. 6**A-C**, top, ○). Four of the six "unsuccessfully" conditioned pairs showed slight increases in the peak area, which were associated with either a

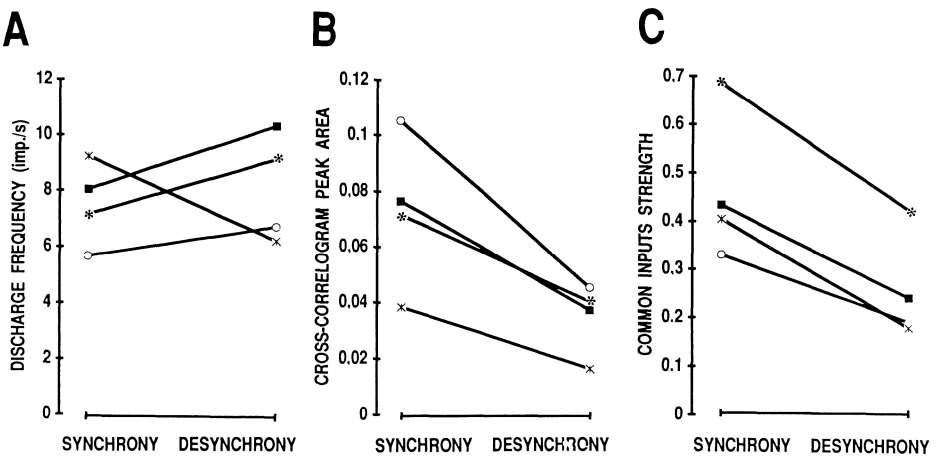

Fig. 8. Values of the geometric mean firing rate (**A**), the peak area (**B**) and CIS (**C**) in successive synchrony and desynchrony conditioning periods are plotted and joined by a line for four MU pairs. Note the consistent decrease of the synchronous activity (peak area and CIS) in the desynchrony conditioning period. The degree of synchronization was greater in the synchrony period than in the control period for one pair (■; cf. Fig. 6) and was not significantly different from control for two pairs (○ and ×; cf. Fig. 6). The remaining pair (*) did not have an adequate preconditioning control period

decrease or an increase in the mean firing rate (Fig. 6**A-C**, bottom).

To investigate whether synchrony of unconditioned MUs also increased during synchrony conditioning, we analyzed the changes in synchronization and discharge frequency for MU pairs recorded concurrently with conditioned pairs. In five instances, a third MU was recorded on the same electrode as one MU of the conditioned pair. The subjects received feedback of the synchronous spikes emitted by the two conditioned MUs, but had no feedback concerning the firing of the third MU. This additional MU and the conditioned MU recorded on the other electrode therefore formed an unconditioned pair. In every instance, the conditioned and unconditioned pairs were related to the same two fingers.

Figure 7 plots the mean discharge frequency, the peak area, and the CIS during the control and synchrony periods for the conditioned pairs (top) and for the unconditioned pairs (bottom) using the same symbols for the conditioned and unconditioned pairs that were recorded simultaneously. There was no consistent change in the peak area and CIS value for three unconditioned pairs (Fig. 7**B**, **C**, bottom, black symbols) recorded simultaneously with three successfully conditioned pairs (Fig. 7**B**, **C**, top, black symbols). An increase in the peak area appeared for one unconditioned pair (Fig. 7**B**, bottom, white diamond) recorded with one unsuccessfully conditioned pair (Fig. 7**A-C**, top, white diamond); however, this pair showed a decrease in the CIS (Fig. 7**C**, bottom, white diamond).

To show that the synchrony feedback itself did not enhance MU synchronization, independently of the subject's conscious effort, we asked two subjects to voluntarily reduce the frequency of the synchrony feedback pulses in four desynchrony conditioning sessions performed after a period of synchrony conditioning. The four tested pairs showed a marked decrease in peak area and CIS during the desynchrony conditioning periods compared with the preceding synchrony period (Fig. 8**B**, **C**). These changes were not associated with any consistent change in firing rate (Fig. 8**A**). These results indicate that the feedback *per se* did not generate synchronous discharge; instead, it seemed that the subjects were able to increase and decrease synchrony of motor unit discharges.

Discussion

In human subjects performing a steady isometric voluntary extension of the fingers, most of the MU pairs recorded in EDC exhibited some degree of synchronous discharge likely to involve common synaptic input. Some parameters of the cross-correlogram peaks were related to MU contractile properties. In addition, the results from conditioning sessions with synchrony feedback suggest that the degree of MU synchronization could be voluntarily altered. These results and their functional implications are discussed below.

Contractile properties

The twitch tensions associated with MU discharges had a wide range of amplitudes and rise times, consistent with the presence of different sizes of MUs. These measured parameters must be considered best estimates in view of the factors that may distort the twitch tension extracted by spike-triggered averaging (Milner-Brown et al. 1973a; Kirkwood 1979; Calancie and Bawa 1986; Nordstrom et al. 1989; Dick 1990; Thomas et al. 1990).

The first source of distortion is mechanical, since the twitches were extracted from the extension force measured by a strain-gauge transducer located about 10 cm from the EDC musculotendinous junction. The mass, velocity, and lever arm of the mechanical linkage tended to reduce the measured contractile force of MUs. This could partly explain the relatively small amplitudes of the twitches that we observed (0.006–3.72 *g*) compared with the larger values (0.3–8.0 *g*) obtained in EDC by direct measurement of the twitch tensions produced by stimulation of single ventral root filament in baboons (Eccles et al. 1968) (assuming comparable MU properties in both species).

A second source of distortion is the partial fusion of successive twitches at higher frequencies (Calancie and Bawa 1986; Nordstrom et al. 1989; Thomas et al. 1990). In cat soleus and medial gastrocnemius muscles, the activation of MUs by electrical stimulation at frequencies of 8–10 imp/s could reduce the TA by 40–75% and shorten the TRT by 10–40% compared with their unfused values

(Calancie and Bawa 1986). To minimize these effects, we compiled spike-triggered averages when firing rates were well below 8 imp/s. The range of contraction times actually found (13–70 ms) encompassed both the fast twitches (15-40 ms) obtained by stimulation of ventral root filaments in the baboon EDC (Eccles et al. 1968) and the slower twitches (40–70 ms) obtained by spike-triggered averaging with firing rates above 10 imp/s in human EDC (Monster and Chan 1977). These studies together suggest that EDC is composed mainly of relatively fast-twitch motor units. Very few MUs have twitches with rise times slower than 60 ms, and these are the ones most affected by fusion (Calancie and Bawa 1986; Thomas et al. 1990).

A third factor that can alter the twitch parameters is the summation of the twitches produced by MUs firing synchronously with the analyzed MU (Milner-Brown et al. 1973a; Kirkwood 1979; Nordstrom et al. 1989; Dick 1990; Thomas et al. 1990). This would tend to increase the apparent amplitude of the twitches educed by spike-triggered averaging and to lengthen the apparent twitch rise times. The total number of motoneurons firing synchronously with each motoneuron spike can be estimated from the mean peak area and the percentage of synchronized MUs (70%). Assuming that EDC consists of 300 MUs (cf. Jenny and Inukai 1983) and that about one-third of EDC motoneurons were recruited at the low force levels at which the MUs were recorded, the number of potentially synchronized motoneurons would be $300 \times 1/3 \times 0.70 = 70$. This number times the mean number of synchronized action potentials per trigger observed for all synchronized pairs (i.e., 0.044) yields the mean number of spikes expected to be synchronized above-chance with any trigger spike during EDC contraction, namely, 3.1 synchronous spikes per trigger. These synchronous twitches are dispersed over the width of the correlogram peak (mean 9.3 ms) and could introduce a significant homogenizing effect on the shape (cf. Dick 1990). Since the dispersion is less than the duration of the twitches, their amplitudes would add, producing an overestimate of the actual motor unit twitch amplitude by a factor of four. In contrast to these predictions, a recent study (Schmied et al. 1992) showed that MUs in the subjects' preferred arm had twitch characteristics similar to MUs in the nonpreferred arm, although synchrony in the former group was almost twice as great.

Given the undetermined amount of distortion from fusion and synchrony, the twitch tensions extracted by spike-triggered averaging represent a first estimate of the motor unit contractile force. Nevertheless, these empirical measures made under comparable conditions, when compared for different units, show the expected correlations (see Milner-Brown et al. 1973b; Rick and Bawa 1992) between MU twitch parameters and mean static force levels: MUs associated with small and slowly rising twitches discharged at the lowest force levels, while MUs with larger and faster rising twitches discharged at the highest force levels. This indicates that, despite the inevitable sources of distortion, two populations of MUs could be differentiated. These two groups of MUs may represent the slow-resistant and fast-resistant MUs, assuming that high-threshold/fatigable MUs were probably inactive in our experimental range. MUs with the slowest and smallest twitch tensions were present in similar proportion to MUs with faster and larger twitch tensions. This is consistent with histochemical analysis revealing that human EDC is composed of 47.3% of type I muscular fibers and 52.7% of type II muscular fibers (Johnson et al. 1973). The fact that the significant amount of synchrony did not abolish these distinctions suggests that synchrony is greater within than between these groups.

Synchronization characteristics

Above-chance synchronization between the discharges of EDC MUs was revealed by the central peaks that occurred in most (70%) of the computed cross-correlograms. This proportion is in the ranges (51–88%) previously reported for hand and forearm muscles, including EDC (Buchthal and Madsen 1950; Dengler et al. 1984; Datta and Stephens 1990; Davey et al. 1990; Bremner et al. 1991a,b; Baker et al. 1992). Synchronization was found for each of the five subjects tested, in proportions ranging from 70% to 82%, with comparable strengths.

Pairs of MUs related to the same finger had a higher incidence of correlogram peaks than pairs related to different fingers, but these peaks were not significantly larger. This suggests that MUs related to different fingers might share fewer inputs, but these are no weaker than those shared by MUs related to the same finger. Thus, the functional compartmentalization in EDC might be reflected more in the distribution than in the effectiveness of the common inputs to different subpopulations of EDC motoneurons (Rick and Bawa 1992).

The durations of the synchronization peaks had a wide range (3–16 ms). An even wider range (up to 30 ms) has been described for pairs of MUs recorded in various hand and forearm muscles, including EDC (Datta and Stephens 1990; Davey et al. 1990; Bremner et al. 1991a,b; Baker et al. 1992), in studies where the peak or the CUSUM rise were delimited visually. A recent review concerning cross-correlation analysis of motoneuron inputs (Kirkwood and Sears 1991) suggests that only the briefest peaks should be ascribed to the process of short-term synchronization by common inputs. More than half of our cross-correlogram peaks had relatively short widths (3–7.5 ms) and, therefore, could be assumed to reflect the action of synaptic inputs shared by motoneurons during voluntary contraction. Short-term synchronization, however, affects not only motoneurons but also the separate sources of input to motoneurons, which can be similarly synchronized by their own common inputs. The resultant secondary coupling of motoneuron discharges by synchronized inputs is likely to be looser than that by common input, leading to broader cross-correlogram peaks. Slightly less than half of our cross-correlogram peaks had widths ranging from 7.5 to 16 ms, which may reflect the combined effects of short-term synchronization through common input and input synchronization.

In agreement with data obtained for cat gamma-motoneurons (Ellaway and Murthy 1985) and human MUs (Dietz et al. 1976; Nordstrom et al. 1992), we observed a negative correlation between the relative peak height k' and the geometric mean of MU firing rates. As proposed by Nordstrom et al. (1992), this might reflect the normalization of the k' parameter by baseline rate more than a physiological relation between the proportion of common inputs and discharge frequency.

The peak area (i.e., number of synchronous spikes above-chance per trigger spike) provides a measure of the strength of short-term synchronization that is less dependent on MU firing rates (Nordstrom et al. 1992). In our study, the range of areas was relatively low (0.014–0.080) compared with ranges reported previously (up to 0.300) in forearm and hand muscles, including EDC (Datta and Stephens 1990; Davey et al. 1990; Bremner et al. 1991a,b; Baker et al. 1992). This could be in keeping with the narrower range of the peak widths observed in our study.

The common input strength (i.e., the frequency of above-chance synchronous spikes) is an index that has been proposed recently to evaluate short-term synchronization independently of MU firing rate (Nordstrom et al. 1992). Indeed, we found no relation between CIS and firing rates. The range of CIS values we observed in EDC (0.095–1.052) is comparable to the range (0.052–1.005) reported during voluntary contraction of the first dorsal interosseus muscle (Nordstrom et al. 1992). Since above-chance synchronous spikes cannot be exclusively ascribed to the action of common inputs, this parameter might be given a more appropriate name such as "synchronous impulse frequency."

A potential source of high synchrony at low firing rates is the possible production of synchronous "mini-twitches" at rates below 3/s. This did not occur in our recordings: motor unit firing rates fell below 3/s in only two instances, and in both cases the associated twitch tensions were the same as those extracted at higher firing rates. Furthermore, the relations between synchronization parameters and motor unit discharge rate were still present when the lowest frequency cases were excluded. Thus, a conceivable low-frequency "ballistic" mode of motor unit activation was not a confounding factor in measures of twitch tension or synchrony.

MU synchronization and contractile properties

The present data provide the first evidence that some parameters of the synchronization of MU discharges during a voluntary contraction are related to the characteristics of their mechanical output. The dependence of the correlogram peak duration and height on MU contractile properties was confirmed by comparing the synchronization of fast and slow pairs. Pairs of MUs that were both slow-contracting had narrower and higher cross-correlogram peaks than pairs of MUs that were both fast-contracting (Table 1).

In the regression analysis, the strongest relation was found between the width of the cross-correlogram peaks and the means of the twitch parameters of each pair. The fast MU pairs that showed the broadest peaks were recorded at the highest level of static force. Similarly, in the first dorsal interosseous muscle, Datta and Stephens (1990) found significantly broader peaks for MU pairs discharging at high force levels than for pairs discharging at lower levels (17.6 ± 6.5 vs 11.3 ± 4.2 ms). As discussed above, broader peaks are likely to reflect the synchronization of inputs. At the high force level at which fast MUs discharged, one could expect activation of more neurons that provide common inputs and more synchronization of the input sources, both common and parallel.

Positive correlations were found between the mean twitch rise times and both measures of the peak height (k' and k). Since the slow and fast pairs discharged at comparable frequencies (Table 1), the higher k' and k values observed for the slower-contracting MUs were not likely to be mediated by differences in discharge frequencies. Indeed, a similar positive correlation was observed between the CIS, which is independent of MU firing rate, and the mean twitch rise times.

A negative trend was observed between the parameters measuring the correlogram peak magnitude (k', k, CIS, area) and the mean twitch amplitudes. However, this relation was much weaker than the relation with the twitch rise time and did not reach significance. This could reflect the fact that the distortions discussed above affected the amplitudes of the twitches more than their rise times.

Only four of the tested pairs included one slow- and one fast-contracting MU. Two of these mixed pairs presented significant peaks in their cross-correlograms, consistent with a widespread distribution of some common inputs to all the motoneurons of a pool (e.g., Mendell and Henneman 1971).

Voluntary control of short-term synchronization

In nine of 15 sessions of synchrony or desynchrony conditioning performed on 12 MU pairs, three subjects succeeded in voluntarily changing the degree of short-term synchronization of MUs with the synchrony feedback. The unsuccessful sessions included the subjects' first exposure to the task. Particularly remarkable was the production of significant correlogram peaks in two of five MU pairs that previously showed no significant synchrony. Increases in the magnitude of MU synchronization, deemed significant on the basis of the difference histogram test, were observed for all categories of MUs, including pairs that were fast, slow, or mixed and related to the same or different fingers. This limited sample would suggest that voluntary control of synchronous activity may involve inputs shared by all types of MUs in EDC.

Although subjects used auditory synchrony feedback, they were generally unable to evaluate their success in modulating the amount of MU synchrony; nor could they describe any conscious strategy used during the successful sessions. They concentrated on the occurrence of the synchrony pulses, rather than on the amount of EDC contraction or the concurrent force output. The same

synchrony feedback was instrumental in both the synchrony and desynchrony sessions. The decreases in peak area and CIS observed in the desynchrony sessions relative to the synchrony session provide significant control against the possibility that the mere presence of the synchrony feedback could directly evoke a change in MU synchronization. Using similar feedback to control MU synchrony on line, Datta et al. (1986) reported that the synchrony feedback "does not alter the strength of the on-going synchronization."

These changes in synchrony must also be compared with the spontaneous increases and decreases in synchronization which have been reported during successive 30 s segments of recording in the first dorsal interosseous muscle (Bremner et al. 1991b). Using longer-duration recordings (15 min, comparable to those in the current study), Nordstrom et al. (1990) did not find a significant trend in the strength of short-term synchronization of masseter MUs. We never observed a decrease of synchrony during the 11 sessions of synchrony conditioning and, in eight of these sessions, the peak area increased. Conversely, no increase in synchronization was ever observed during the four desynchrony sessions and, in each case, the peak area was clearly reduced in the period of desynchrony conditioning. Coincidental changes in short-term synchronization are highly unlikely to account for the consistently appropriate changes during the synchrony and desynchrony conditioning periods.

The subjects could have increased the number of synchronous firings in a trivial manner by increasing the firing rate of both MUs, thus producing a proportional increase in the rate of coincidental firing by chance (Clark et al. 1981). However, this could not explain the observed increases in the relative measures of peak height (MPI, k' and k) that are normalized to baseline. Moreover, increases in synchrony occurred concurrently with decreases *or* increases in background rate of the conditioned pairs, and comparable changes in firing did not mediate changes in the synchronization of unconditioned pairs. The fact that two of five unconditioned units decreased their firing rates is consistent with a previous report that during voluntary activation of a single MU monitored by feedback, the neighboring MUs were progressively silenced (McCord et al. 1974).

Since the relative measures of the peak heights (k, k', MPI) are inversely related to the mean MU firing rate, the relative measures of synchrony could be increased by reducing the baseline firing rate while keeping the peak area constant. This did not appear to be the general case: the firing rate was reduced in only two of the five successful sessions. The present data show that the changes in the synchronous firings produced by the subjects could not be attributed to general changes in the firing level of the cross-correlated MUs (see also Bremner et al. 1991b). Instead, these changes were probably mediated by volitional control over common input producing MU synchronization.

These results can be compared with the increases in short-term MU synchronization described after several weeks of training in maximum isometric contractions of the first dorsal interosseous muscle (Milner-Brown et al. 1975). A concurrent increase in the transcortical reflex response to electrical stimulation of the median nerve led the authors to suggest that "supraspinal connections from the motor cortex directly to motoneurons may be enhanced as a result of training to the point where they produce a significant synchronization of motor units" (Milner-Brown et al. 1975). The present changes in short-term synchronization were detected in the course of the conditioning session and must reflect rapid alterations in the relative contributions of common inputs. One direct mechanism would involve a change in the proportion of descending monosynaptic input, such as the corticomotoneuronal cells that strongly affect EDC motoneurons (Phillips and Porter 1977; Fetz and Cheney 1980). The effectiveness of common inputs in synchronizing motoneuron activity may also be modified indirectly. Monoaminergic bulbospinal pathways have been shown to inhibit short-term synchronization of cat gamma-motoneurons (Davey and Ellaway 1988): a similar action has been postulated for alpha motoneurons (Baker et al. 1992). Indirect control of MU synchronization might also be mediated by supraspinal modulation of the Renshaw decorrelating action (Gelfand et al. 1963; Adam et al. 1978), or by enhanced activity of spindle afferents via selective activation of gamma-motoneurons (Rudomin 1989). These possibilities suggest further experiments to resolve the neural mechanisms by which humans could rapidly alter short-term synchrony of MUs and, by implication, control the proportion of last-order common inputs to motoneurons.

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