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RESEARCH ARTICLE

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EMG activation patterns during force production in precision grip. III. Synchronisation of single motor units

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Abstract Motor unit (MU) synchronisation during isometric force production in the precision grip was analysed in five subjects performing a visually guided step-tracking motor task with three different force levels. With this aim multi-unit electromyographic (EMG) activity of 14 intrinsic and extrinsic finger muscles from 15 experimental sessions was decomposed into the potentials of single MUs. The behaviour of 62 intrinsic and 30 extrinsic MUs in the motor task was quantified. Most MUs displayed a positive correlation between firing rate and grip force. Compared to MUs in extrinsic muscles, intrinsic MUs had steeper regression lines with negative intercepts indicating higher force sensitivity and higher recruitment thresholds. A cross-correlation analysis was performed for 69 intra- and 166 intermuscular MU pairs while steady grip force was exerted at the three force levels. Synchronisation, for at least one force level, was found in 78% of the intra- and 45% of the intermuscular pairs. The occurrence of synchronisation was not stable over the force range tested. Factors influencing the fluctuations in occurrence and strength of synchronisation were investigated. Force increase was not paralleled by increased synchronisation; in contrast, in most MU pairs, especially intermuscular pairs, synchronisation occurred preferentially at the lower force levels. The recruitment threshold appeared to play a determining role in synchronisation: the more similar the thresholds of two MUs, the greater the probability of them being synchronised at this force level. Synchronised MUs fired on average at a lower frequency than non-synchronised ones. Finally, synchronisation at the multi-unit EMG level does not indicate that all underlying MUs are synchronised, nor does the absence of temporal coupling at the multi-unit level indicate that none of the MUs is synchronised.

Key words Hand · Isometric force · Precision grip · Motor unit · Synchronisation · Muscle synergy · Human · Cross-correlation

Introduction

The precise control of the hand muscles contributing to grip force, in particular to precision grip force, is a prerequisite for fine manipulative actions. The large number of muscles impinging on the thumb and index finger leads to an excess of the degrees of freedom of the musculoskeletal system with regard to the controllable forces and moments at the fingertips and thus represents a biomechanically redundant system. Therefore, a desired grip force can theoretically be generated by an infinite number of muscular activation patterns. It has been put forward that grouping several muscles or motor unit (MU) pools together in a synergistic way might be a mechanism of the central nervous system (CNS) to reduce and simplify this redundancy (for a review see Gielen et al. 1995). A means by which this synergy could be achieved is by time-locking the activation of several muscles, muscle compartments, or MU pools. At the MU level, time-locking would lead to the synchronisation of MUs within muscles and between synergistically active muscles.

Indeed, it has been shown that synchronisation occurs between MUs and MU populations more often than can be expected by chance alone. Short-term synchronisation has been uncovered in many different muscular systems at the single MU and multi-unit EMG level: in the respiratory system (Sears and Stagg 1976), in the trigeminal system (Nordstrom et al. 1990; Türker et al. 1996; DeLuca et al. 1993), in the trunk musculature (Carr et al. 1994), and in the upper and lower limb muscles (Dietz et al. 1976; Datta and Stephens 1990; Datta et al. 1991;

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Table 1 Overview of the muscles with innervation and number of motor units analysed in the present study (innervation according to Feneis 1988)

Muscle	Abbreviation	Innervation	No. of MUs
Thumb muscles			
Abductor pollicis brevis	AbPB	Median	1
Abductor pollicis longus	AbPL	Radial	4
Adductor pollicis	AdP	Ulnar	18
Extensor pollicis brevis	EPB	Radial	6
Extensor pollicis longus	EPL	Radial	1
Flexor pollicis brevis	FPB	Median/ulnar	5
Flexor pollicis longus	FPL	Median	7
Opponens pollicis	OPP	Median	7
Index finger muscles			
First dorsal interosseus	1DI	Ulnar	16
First lumbricalis	1LUM	Median	8
First palmar interosseus	1PI	Ulnar	7
Extensor digitorum communis	EDC	Radial	3
Flexor digitorum profundus	FDP	Median	4
Flexor digitorum superficialis	FDS	Median	5

Bremner et al. 1991b; Nordstrom et al. 1992; Schmied et al. 1993; Maier and Hepp-Reymond 1995b). Notably, Bremner et al. (1991a, 1991b) demonstrated for a large variety of hand and forearm muscles a very robust synchronisation of MU activity with a narrow central peak in the cross-correlograms in 88% of the pairs studied.

These results have mostly been gained in experiments with visual and/or auditory feedback of at least one of the activated MUs. In addition, in most cases only simple movements around one joint were investigated. We thus wanted to investigate to what extent MU synchronisation is present and robust in a more natural, behavioural task in which the subjects are not aware of the motor unit activity underlying force production, but only obtain feedback of the grip force exerted between the tips of the thumb and index finger. Furthermore, we wanted to find out which MU characteristics could account for the relatively small degree of temporal coupling and the fluctuating and unstable muscle synergies demonstrated by Maier and Hepp-Reymond (1995b) with multi-unit electromyography (EMG) during grip force.

The present analysis was performed on a selection of the data presented and discussed by Maier and Hepp-Reymond (1995a, 1995b). We show that synchronisation occurs during the production of force in the precision grip in pairs of intra- and intermuscular MUs of the hand muscles, preferentially in MU pairs with similar recruitment levels and at forces just above recruitment, but with a striking variability across the various levels of force and muscle activation.

Materials and methods

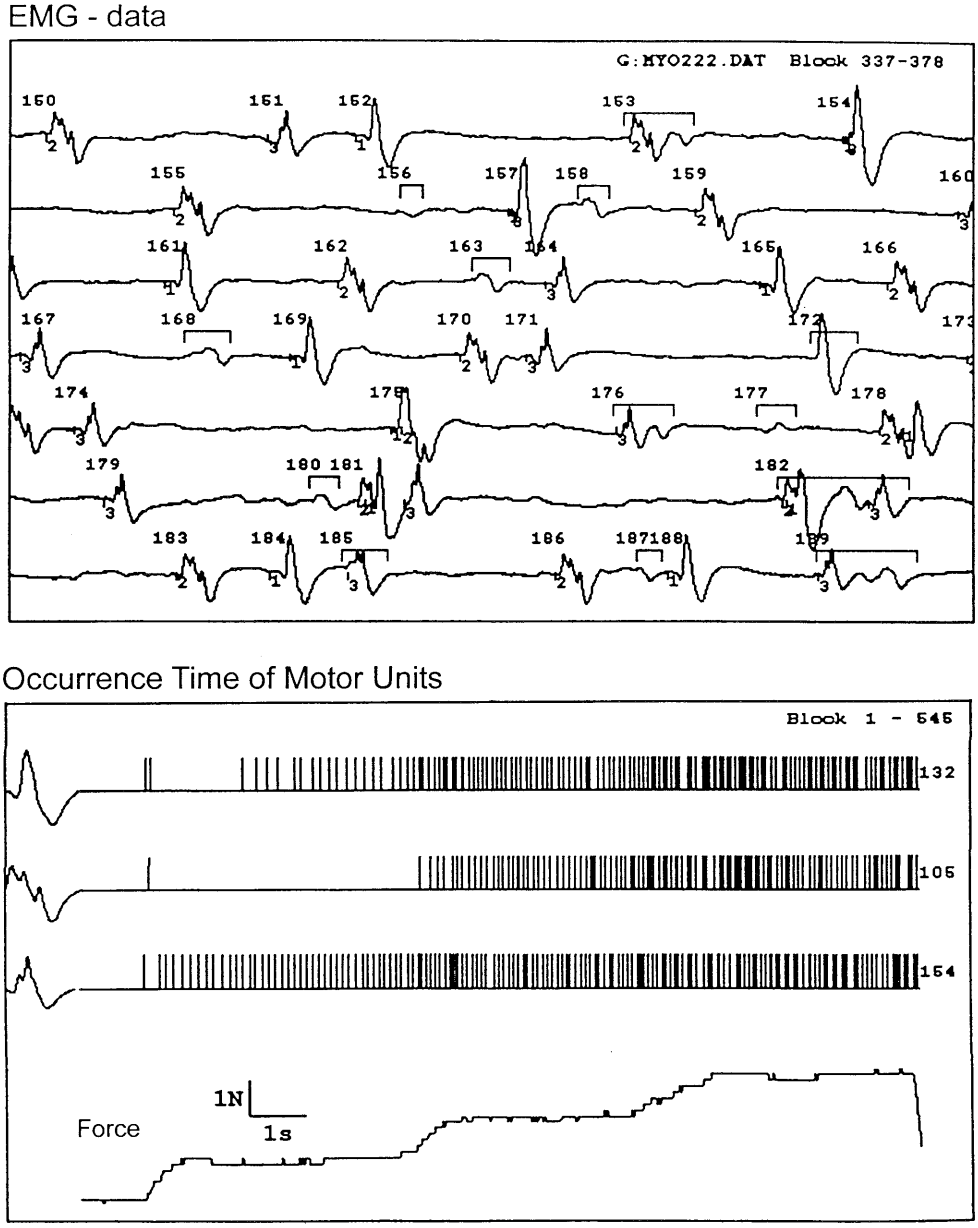
This analysis is based on a subset of the data gained in the experiments of Maier and Hepp-Reymond (1995a, 1995b) at the multi-unit EMG level. The current sample was selected to obtain a maximal variety of muscle combinations. The muscles, their abbreviations and the quantity of MUs analysed in this paper are listed in Table 1. The experimental setup, task, EMG and force recording procedures are identical to those described in these two papers.

In brief, five healthy subjects had to perform a visuomotor step-tracking task by exerting isometric force on a transducer which was held between the tips of thumb and index finger, and by matching three consecutive target forces (1, 2 and 3 N, i.e. less than 10% maximum voluntary contraction, MVC). In each trial the whole sequence of required target forces was displayed on a screen in front of the subject while the exerted force was represented as a running cursor. The EMG signals, recorded with bipolar, intramuscular needle electrodes, and three force signals (thumb, index and resultant total force) were stored on an FM tape for later offline analysis.

Data acquisition and EMG decomposition

The data of one experimental session consisted of up to four multi-unit EMG records (10 kHz sampling frequency/channel, 50 Hz notch and anti-aliasing filtering at 3 kHz), and the resultant force (40 Hz sampling frequency; gain: 1 V/N, 0.13 N resolution; range: ±5 N) acquired from 20 trials of 15 s duration. The limited time and amplitude resolution of the force channel were determined by the software and hardware configuration of the data acquisition system and could not be adjusted. This system (ARTMUP, Haas and Meyer 1989) decomposed the EMG signals into the constituent MU potentials (MUPs, see Fig. 1). The ARTMUP system of discriminating MUPs within a multi-unit EMG signal is based on several phases. First, the algorithm detects segments of activity (Fig. 1, top panel) in the multi-unit EMG where the signal exceeds a background level of activity. These segments putatively contain one or more MUPs. In the next phase the algorithm extracts templates for single MUPs from these segments by a nearest-neighbour cluster analysis considering the following MUP features: maximal positive amplitude, peak-to-peak amplitude, area, duration of an active segment, maximal positive slope, maximal negative slope, number of extremes. Finally, with the estimated mean repetition rate, superimposed potentials are automatically decomposed by subtracting and shifting the templates from the summed signal (for details see Haas and Meyer 1989). The user can also control and interactively optimise the results of the program by checking the interpotential interval histogram for plausibility and by subtracting single potentials from overlapping potentials.

In the low force range used in this investigation (<10% MVC), the ARTMUP system reliably detected up to four different potentials in one EMG channel (single electrode recording). In 18 channels one MU was discriminated, in 12 channels two MUs, in 14 channels three MUs and in two channels four MUs. Full decomposition into the constituent MUs was achieved for 78% of a total of 178,713 segments with valid data. For the remaining 22% partial decomposition was achieved.



EMG - data

Occurrence Time of Motor Units

Fig. 1 Example of EMG decomposition by ARTMUP. The multi-unit EMG of an adductor pollicis is decomposed into three constituent MU potentials. *Top panel* Original EMG signal of 1.05 s duration (seven lines of 0.15 s each) at the 2-N level after segmentation, cluster analysis and detection of superimposed MUPs. *Numbers above the signal traces* (*150–189*) indicate the identified segments; beneath are the successfully discriminated MUPs (*1, 2 and 3*). Not completely decomposed data segments are denoted by *a square bracket*. *Bottom panel* Occurrence times of the three discriminated MUs in one 15-s trial with the corresponding force trace

The occurrence times of the MUPs were printed out in raster form with the respective force traces, peri-response time histogram and interpotential interval histogram (Fig. 2).

Data selection

For each trial three epochs of 3 s each, one per force level, were automatically selected under the criterion of the smallest residual error between applied force and target force. The transient force steps from one level to the next were not used, since stationary data are a prerequisite for the cross-correlation method. The occurrence times of the MUPs and the mean grip force produced during these epochs were extracted for further processing.

Motor unit behaviour

The contribution of the MUs to force control was estimated by correlating the mean firing rate with the mean applied force of each epoch. Scatter diagrams with a maximum of 60 data points per experimental session (20 trials × 3 steps) were created for all MUs, with the three data points of each trial connected to visualise the stability of the firing rate/force relationship over the trials (see Fig. 3A,B). For each MU a correlation and regression analysis between force and firing rate was performed. The values for the slopes and y-axis intercepts of the force/firing rate regression lines for the intrinsic and extrinsic MUs are summarised and displayed in the cumulative plots of Fig. 3C,D. The *single trial* recruitment level of the MUs was defined interactively as the lowest steady-state force level, i.e. 1, 2 or 3 N, at which the MU activity was stable and regular. Subsequently, a single *recruitment threshold* was calculated for each MU by averaging the single trial recruitment levels. To classify the MU, this value, rounded-up, was taken as its overall *recruitment level*, i.e. 1, 2 or 3 N.

Motor unit synchronisation

To detect the existence of synchronised discharge of MU pairs, a cross-correlation analysis was performed for both intra- and inter-

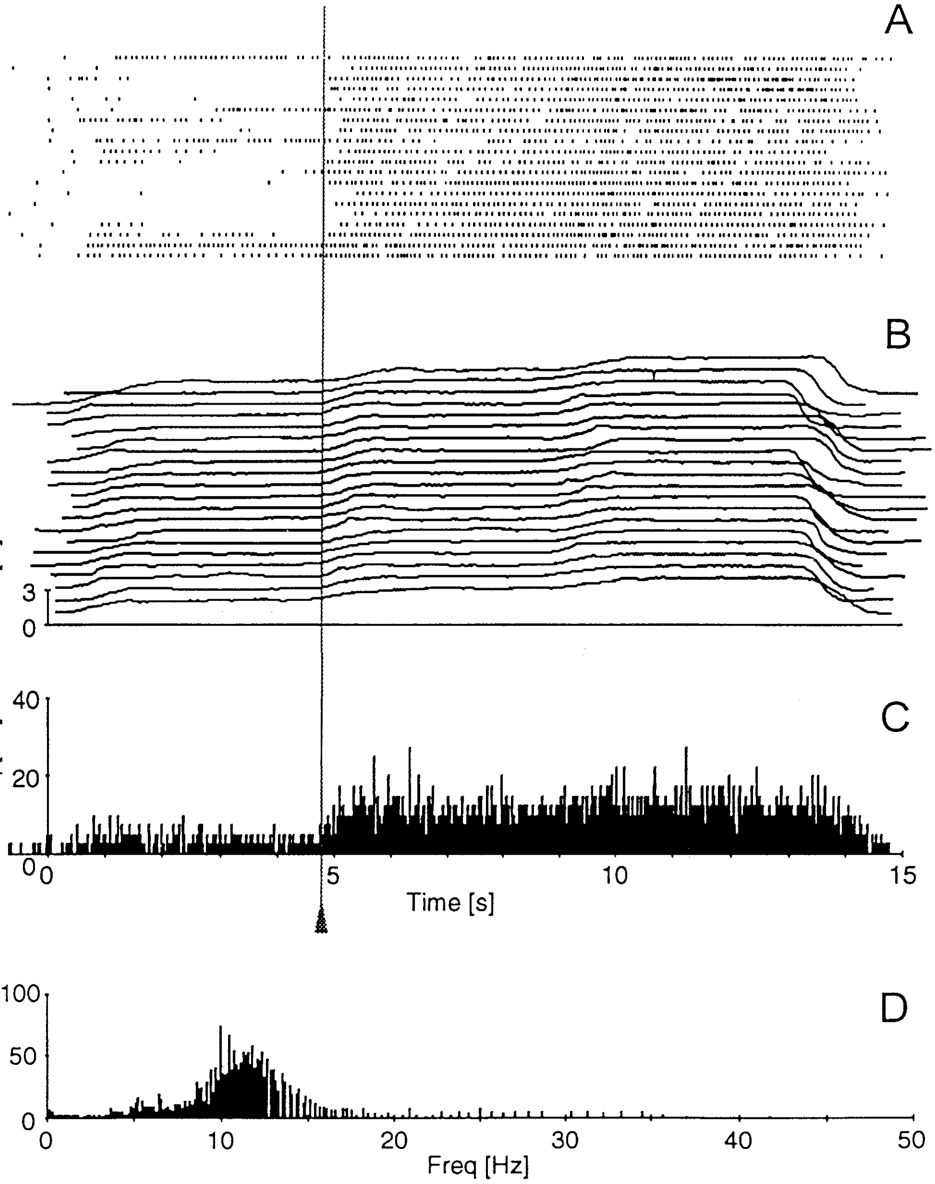


Fig. 2A–D Opponens MU activity during 20 trials. This MU was one of four others that were discriminated within the multi-unit EMG signal. **A** Raster histogram of the MUP train. The variability of recruitment may be due to different contraction rates of the muscles since this parameter was not controlled in the experiment. **B** Force traces. **C** Peri-response time histogram. *Vertical line* indicates the point of alignment, i.e. the onset of force increase from 1 N to 2 N. The MU-firing rate clearly increases with force (correlation coefficient *r*=0.80). **D** Interpotential interval histogram showing a unimodal distribution of the firing frequency even though the data are derived from all three force levels

muscular pairs on each force level separately and for a maximum of 20 trials, provided that a minimal number of 200 MUPs/channel was given. Thus a maximum of three cross-correlations/MU pair could be obtained for further analysis. The cross-correlation was calculated using Spike2 software (CED, Cambridge UK) on a time interval of ±100 ms with a bin width of 2 ms. Except for the choice of the bin width and the calculation of the CUSUM baseline, we used identical methods and criteria for evaluating cross-correlograms as did Bremner et al. (1991a). To partly account for the higher variance of the cross-correlograms due to the relatively low number of trigger spikes, a bin width of 2 ms was used. The CUSUM baseline calculation was restricted to a short averaging period of ~100 ms in order to avoid boundary effects due to the relatively short 3-s force holding period and to avoid contamination by secondary peaks or by troughs after the peak. The search for significant short-term synchronisation peaks was confined to a time window of ±20 ms around time-lag zero. A first baseline was defined as the average amplitude at lag times –100 to –50 and +50 to +100 ms. The peak was determined as that period in the cumulative sum derivative (CUSUM, cf. Davey et al. 1986) where the largest continuous inclination was found, i.e. between the two inflections of the CUSUM. In a second iteration the baseline was recalculated using the bin values from –100 ms to the peak onset, thus avoiding postspike troughs. The CUSUM and the peak were recalculated with the new baseline. A peak was accepted when the CUSUM exceeded the significance limits based on the variance of either Poisson or stochastic point processes (3 times standard deviation of the Poisson or stochastic point process, respectively), whichever was smaller. The cross-correlogram and CUSUM are displayed together with the significance limit (Fig. 4). To determine the synchronisation strength the peaks were quantified using two main indices: *k* or relative peak amplitude (Sears and Stagg 1976) and *k'* or relative peak area (Ellaway and Murthy 1985*)*. In contrast to Vaughan and Kirkwood (1997), the peak width was defined as the time period between start and end of the inclination in the CUSUM, and not as the half-width of the peak in the cross-correlogram.

The robustness of the CUSUM calculation for evaluating significance of cross-correlogram peaks was demonstrated by Bremner et al. (1991a) with segments of independent records of 100 trigger pulses each, i.e. half of the 200 spikes we specified as minimum criterion: they showed a faulty estimation in less than 1% of the 360 cases.

Furthermore, the intermuscular MU cross-correlograms were compared with the cross-correlograms of the corresponding multi-

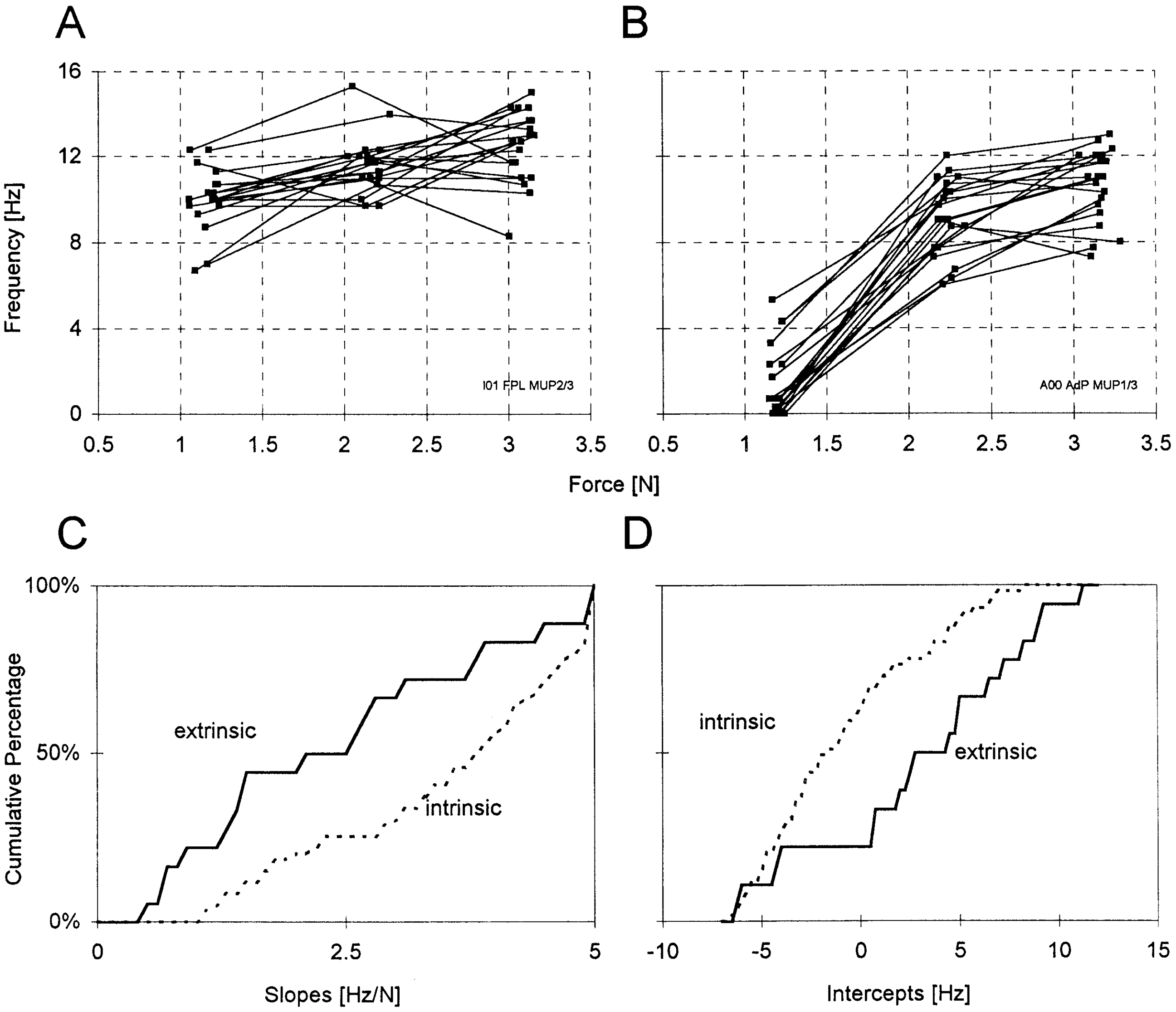


Fig. 3 Relationship between firing rate and force for one FPL MU **(A)** and one AdP MU **(B)**, and for populations of intrinsic and extrinsic MUs **(C,D)**. **A** The firing rate as a function of force for the FPL MU shows a shallow slope and a high intercept, typical for extrinsic MUs. **B** In contrast, the AdP MU has a steeper slope and lower intercept, typical for intrinsic MUs. **C** Cumulative percentage calculated from the values of the slope of the force/firing rate regression lines for 59 intrinsic (*stippled lines*) and 18 extrinsic (*continuous lines*) MUs. About 50% of the extrinsic MU population has a slope below 2 Hz/N in contrast to less than 20% of the intrinsic MUs, indicating a generally steeper slope for intrinsic MUs. **D** Cumulative percentage of the intercepts of the force/firing rate regression lines for intrinsic and extrinsic MUs. About 63% of intrinsic MUs show negative intercepts, indicating recruitment during the increase of force, whereas most extrinsic MUs have positive intercepts due to activity prior to 1 N

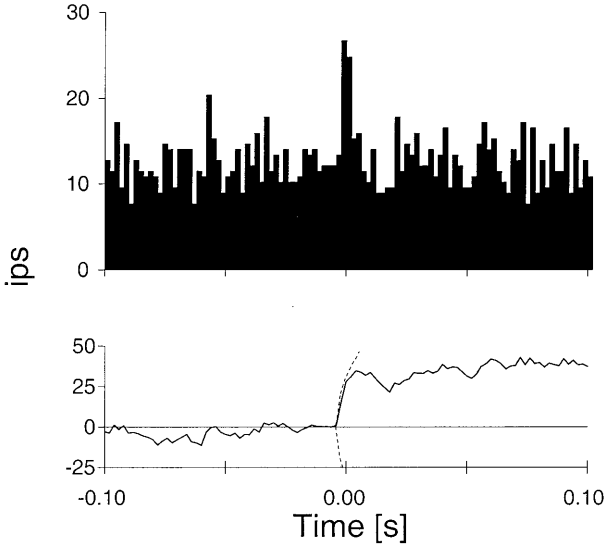


Fig. 4 *Top* Cross-correlogram of two AdP MUs on the 2-N level ▶ with peak centred at time 0. *Bottom* Corresponding cumulative sum derivative (CUSUM, *heavy line*) with confidence limits (*dashed lines*) showing significant short-term synchronisation. Same MUs as MU1 and MU2 of Fig. 1. The mean firing rates were 10.1 and 11.0 impulses/s (*ips*), respectively. The number of triggers contributing to the cross-correlogram is 559 for MU1 and 547 for MU2. Synchronisation index *k*: 3.00

unit EMGs obtained from Maier and Hepp-Reymond (1995b). In brief, cross-correlations between EMG activity of two muscles were computed by multiplying the Fourier transform of the EMG from one muscle by the complex conjugate of the other muscle's Fourier transform of the EMG. This product was then inversely transformed and summed over all trials of a single force level. Muscle activity was considered synchronous if the size of the peak exceeded four standard deviations of the total signal.

Results

Motor unit sample and behaviour

The data were gained in 15 experimental sessions from five healthy subjects. The discrimination of the selected multi-unit EMG signals yielded 92 MUs, 30 located in extrinsic, 62 in intrinsic muscles.

Of the 92 MUs, 29 were tonically active already at the 1 N level, 42 MUs were recruited between 1 and 2 N, and 21 MUs above 2 N. The mean firing rates varied between 5 and 14 Hz for the 1–3 N force range. The mean firing rate at recruitment threshold was 8.6±1.9 Hz.

Four statistical values were compared to show the differential contribution of extrinsic and intrinsic MUs to grip force: the recruitment threshold, the correlation coefficient of the force/firing rate relationship, the slope and the intercept of the corresponding regression analysis. For the former two values all 92 MUs were taken into account, for the latter two only the 77 significantly and positively correlated MUs.

First, the mean recruitment threshold was 1.4±0.7 N (range: 0.2–2.9 N). The recruitment thresholds were significantly lower for the extrinsic MUs as compared to the intrinsic ones (1.0±0.6 N, n_{extr}=30 vs 1.6±0.7 N, n_{intr}=62, respectively; *t*-test, $P<0.001$).

Second, 77 MUs showed significant positive correlation coefficients (18 extrinsic and 59 intrinsic MUs). Significant negative correlations were found in three extrinsic and one intrinsic MUs. The activity of 11 MUs, nine extrinsic and two intrinsic MUs was unrelated to the resultant grip force in the task. Further differences between intrinsic and extrinsic MUs were: (a) relatively more MUs of intrinsic muscles displayed a significant force/firing rate relation than extrinsic MUs (intrinsics: 60 out of 62, 97% vs extrinsics: 21 out of 30, 70%, χ^2-test, $P<0.001$); (b) the MUs of intrinsic muscles showed a significantly better positive correlation than the extrinsic MUs (r_{intr}: 0.68±0.17, n=59; r_{extr}: 0.57±0.22, n=18; *t*-test, $P<0.05$); (c) with regard to positive significant correlations, the MUs of intrinsic muscles had a smaller scatter in the force/firing rate relationship (variance σ^2 of correlation coefficient r=0.028, n=59) in comparison to the MUs of extrinsic muscles (variance σ^2: 0.049, n=18). However, this difference was not significant (*F*-test, $P>0.05$).

Third, the slopes of the regression lines for 77 positively correlated MUs varied between 0.5 and 6.0 Hz/N, with an average of 3.3±1.5 Hz/N. The slopes of the intrinsic MUs were steeper (3.56 Hz/N vs 2.45 Hz/N) when compared with the extrinsic ones (*t*-test, $P<0.01$, n=77). The slope of the four negatively correlated MUs had a range of –1.0 to –1.3 Hz/N.

Finally, the *y*-axis intercepts of the intrinsic MUs were more negative (–0.92 Hz vs 2.91 Hz) when compared with the extrinsic ones (*t*-test, $P<0.001$, n=77). Negative intercepts are indicative of recruitment at higher force levels within the investigated force range.

In Fig. 3, the two exemplary scatter diagrams and the two cumulative plots of the slopes and intercepts, the latter originating from the significant positive force/firing rate regression lines, highlight the differences between the MUs in intrinsic and extrinsic muscles. Panel C (cumulative plot of slope values) shows that the intrinsic MUs have steeper slopes, i.e. the cumulative graph of the intrinsic MUs is shifted more to the right compared to the extrinsic one. Panel D demonstrates that the *y*-intercept values for the intrinsic MUs are more negative. The cumulative graph of the intrinsic MUs is, therefore, shifted to the left in comparison to the extrinsic graph.

Motor unit synchronisation

To detect the synchronisation between two MUs the respective times of MUP occurrence were cross-correlated. Narrow peaks in the cross-correlograms around time zero, indicating synchronised activity, were found in the majority of the cases.

Intermuscular motor unit synchronisation

Out of 328 possible MU pairs resulting from the 92 analysed MUs, 166 intermuscular pairs could be gained with simultaneously active MUs. In 59 pairs the MUs were coactive on one force level only, in 68 pairs on two levels and in 39 on all three levels, yielding 312 cross-correlograms. Synchronisation was found on at least one force level in 45% (75) of the MU pairs: 65 pairs on one, nine pairs on two, and a single pair on three levels, yielding 86 cross-correlograms with significant synchronisation peaks. The mean and standard deviation of the synchronisation strength was given by the indices *k:* 2.19±0.50, and *k':* 1.70±0.30 (n=86).

Intramuscular motor unit synchronisation

From a total of 83 intramuscular MU pairs, 69 pairs were accepted for further processing. In 22 pairs the MUs were coactive on only one level, in 27 pairs on two levels and in 20 on all three levels, yielding 136 cross-correlograms. Fifty-four MU pairs (78%) showed significant synchronisation on at least one force level. Among these, only four pairs were synchronised on all three force levels (2 AbPL, 1 AdP and 1 FPL pairs), 15 at two and 35 at one level only, yielding 77 cross-correlograms with significant synchronisation peaks. The mean and standard deviation of the synchronisation strength was

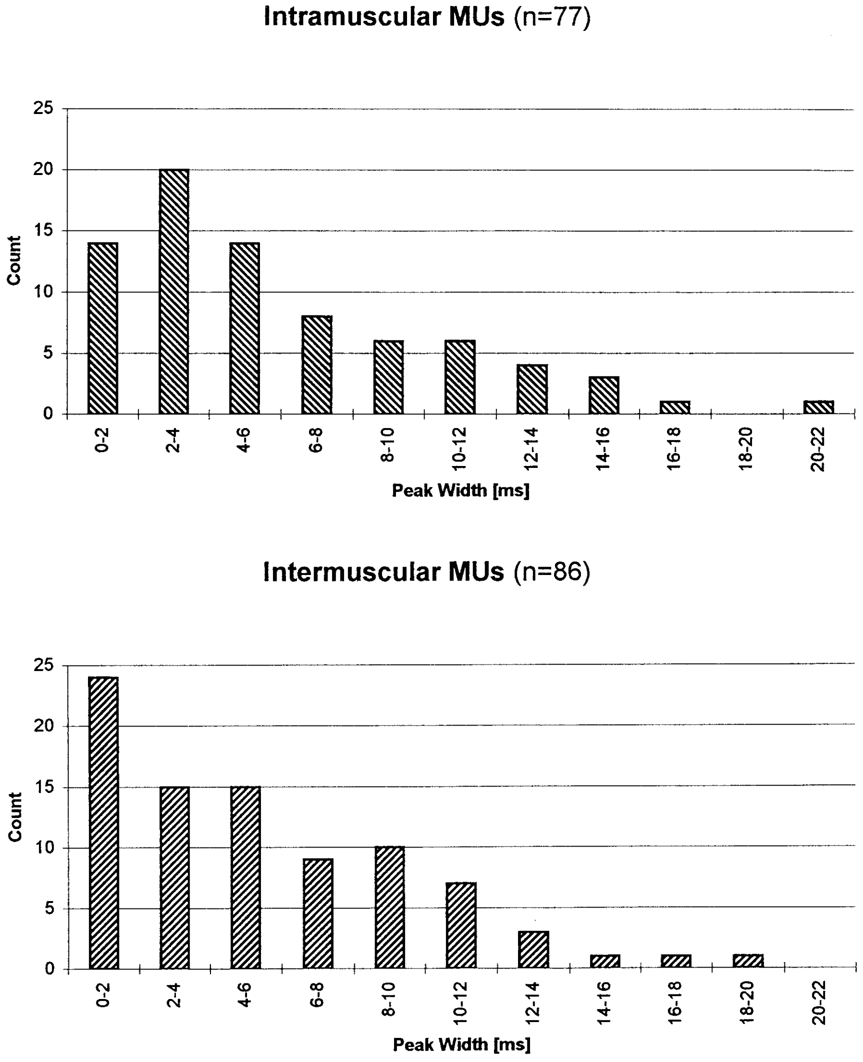


Fig. 5 Distribution of the cross-correlation peak widths determined at the base of the peak for intramuscular (*top*) and intermuscular (*bottom*) pairs. About 50% of the intramuscular and 40% of the intermuscular pairs have peak widths smaller than 6 ms, indicative of monosynaptic effects mediated by branched last-order fibres

given by the indices *k:* 2.49±0.88, and *k':* 1.81±0.46 (n=77).

Comparison of intra- and intermuscular synchronisation

The percentage of synchronised MU pairs was significantly larger for the intramuscular pairs than for the intermuscular ones (intramuscular: 54 out of 69 vs intermuscular: 75 out of 166, χ^2-test, $P<0.001$). The synchronisation strength was also significantly stronger for the intramuscular pairs (t-test, $P_k<0.01$; $P_{k'}<0.05$, n=163). There was no significant difference in mean peak width between intra- and intermuscular MU pairs (7±4 vs 6±4 ms, *t*-test for means, Kolmogoroff-Smirnoff-test for the distribution, Fig. 5). The median peak width was 6 ms for both populations (see "Materials and methods"). There was no correlation between the number of spikes (geometrical mean of the two MUs in a pair) and the peak width in the cross-correlograms (r=0.081, $P>0.05$, n=163).

Factors influencing synchronisation

We attempted to elucidate some of the factors, such as innervation, anatomical location, and mean recruitment level, that could possibly influence MU synchronisation in the present experimental situation.

Innervation and anatomical location

We first tested the hypothesis according to which the innervation by the same nerve would increase the probability of synchronisation in intermuscular MU pairs. The pairs innervated by the same peripheral nerve had significant peaks in 45% of the 76 cross-correlograms. The probability of synchronisation in pairs with different innervation reached a similar percentage (46%, n=90).

Secondly, the *intramuscular* pairs, with both MUs belonging to either an intrinsic or an extrinsic muscle, were more often synchronised than MUs in *mixed* intermuscular pairs (intrinsic: 37/45; extrinsic: 17/24; mixed: 20/58;

Table 2 Occurrence and strength of synchronisation in all intra- and intermuscular MU pairs grouped according to their location in intrinsic or extrinsic muscles (*top)* and in thumb or index finger muscles (*bottom*) (*Sync.* synchronised MU pair, *$P<0.05$, ANOVA, see text)

	Intrinsic pairs			Mixed intrinsic/ extrinsic pairs			Extrinsic pairs			Thumb pairs			Mixed thumb/ index finger pairs			Index finger pairs		
Occurrence	*n*	Sync.	%	*n*	Sync.	%	*n*	Sync.	%	*n*	Sync.	%	*n*	Sync.	%	*n*	Sync.	%
Total	132	82	62	58	20	34	45	27	60	73	52	71	103	47	46	59	30	51
Strength																		
Index *k*	2.13±0.39			1.94±0.30			2.72±0.66*			2.36±0.71			2.11±0.35			2.20±0.56		
Index *k'*	1.70±0.28			1.54±0.18			1.94±0.35*			1.76±0.36			1.69±0.29			1.66±0.24		

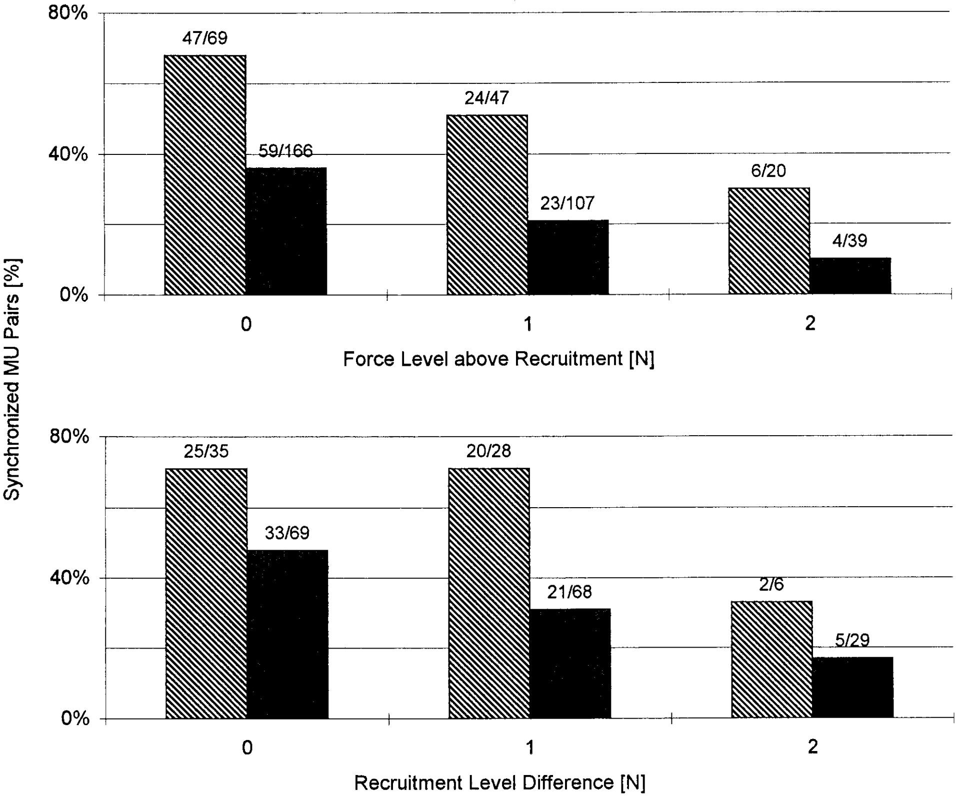


Fig. 6 Synchronisation at levels above recruitment (*top*) and in function of the difference between the recruitment levels of the two MUs in a pair (*bottom*). The synchronisation probability decreases as force increases above recruitment (*top*). The larger the difference between the two recruitment levels, the smaller is the synchronisation probability (*bottom)* (intramuscular pairs *in grey*, intermuscular pairs *in dark columns*)

χ^2-test; $P_{intr}<0.001$, $P_{extr}<0.01$). The *intermuscular* pairs, with both MUs belonging to either an intrinsic or an extrinsic muscle, were more often synchronised than the mixed MU pairs (intrinsic: 45/87; extrinsic: 10/21; mixed: 20/58; χ^2-test, $P_{intr}<0.05$, $P_{extr}<0.05$). When all MU pairs (intra- and intermuscular) were analysed together, the synchronisation was significantly stronger in the extrinsic than in the intrinsic or mixed MU pairs (ANOVA, $P<0.05$, Table 2).

Thirdly, intramuscular MU pairs in *thumb* muscles had a higher probability of synchronising than intramuscular MU pairs of *index finger* muscles (thumb: 36/41; index: 18/28; χ^2-test, $P<0.05$). This was not the case for intermuscular MU pairs (thumb: 16/32; index: 12/31; χ^2-test, $P>0.05$). With respect to the synchronisation strength, no further significant differences were found between thumb and index finger MU pairs, neither for intra- nor for intermuscular pairs. The data are summarised in Table 2 with no distinction between intra- and intermuscular MU pairs.

Influence of recruitment level

The MU pairs were classified according to the recruitment level of the MU with the higher level in the pair (i.e. lowest level of stable firing: 1, 2 or 3 N), and the occurrence of synchronisation was analysed with respect to the force levels above this recruitment. A higher probability of synchronisation could be shown at the level where recruitment occurred regardless of the absolute force. Among the intramuscular pairs, synchrony was mainly found at recruitment in 47 out of 69 pairs (68%) or at one force level above recruitment (24 out of 47 pairs, 51%). Only 30% (6 of 20 pairs) were synchronised at two levels above recruitment. The same trend was also observed for the intermuscular pairs: 36% (59/166) at recruitment, 21% (23/107) and 10% (4/39) for two and three force levels above recruitment, respectively (Fig. 6). This finding was highly significant (χ^2-test, $P<0.01$ for intra- and $P<0.001$ for intermuscular pairs).

Furthermore, we checked whether the difference between the recruitment level of the two MUs in a pair affected synchronisation. The MU pairs were grouped into three classes: pairs with no difference in recruitment level between their two MUs, and pairs with a difference of one and two force levels. MUs with a similar recruitment level were firing synchronously in 71% of intra- and 48% of intermuscular pairs (25/35 and 33/69 pairs, respectively). Among the MU pairs with one force level difference, 71% of intra- and 31% of intermuscular pairs showed synchrony (20/28 and 21/68 pairs, respectively). Finally, synchronisation occurred only in a minority of pairs with a difference of two levels (33% of intra- and 17% of intermuscular pairs, i.e. 2/6 and 5/29 pairs). This higher synchronisation probability with small differences in recruitment level was, however, only significant for the intermuscular pairs (χ^2-test, $P<0.01$, Fig. 6, bottom).

Stability of synchronisation

Synchronisation on all three force levels was observed only in five out of 235 intra- and intermuscular MU pairs, and only 24 pairs showed synchronous firing on two force levels.

The two variables that determine the overall MU behaviour in force production are recruitment and rate coding. If, as suggested by our data, the recruitment level is a determining factor in synchronisation, we can make two predictions that should account for the instability in synchronisation over the force range tested. First, because most MUs were recruited at low forces, synchronisation should occur preferentially at low force levels with, as a consequence, a loss of synchrony at higher forces and higher firing rates. Secondly, synchronised MU pairs should generally display lower firing rates than non-synchronised ones.

Table 3 Occurrence of synchronisation in 93 MU pairs (intra- and intermuscular) with activity on at least two levels grouped according to their distribution in the four classes *low*, *high*, *stable* and *alternating*, as explained in the text

	n	Low	High	Stable	Alternating
Intramuscular	39	17*	6	15	1**
Intermuscular	54	29***	11	7	7
Total	93	46***	17	22	8***

*$P<0.05$, **$P<0.01$, ***$P<0.001$; *F*-test

These two predictions could indeed be confirmed. To analyse the relationship between exerted force and synchronisation stability, only those MU pairs with both MUs activated on at least two force levels were taken into account (93 intra- and intermuscular MU pairs). The MU pairs were grouped into four mutually exclusive classes: *low, high, stable, alternating* (Table 3). The “low” class contained the MU pairs that were synchronised only on the lower force level but not on the higher ones. For the class of “high” pairs, synchronisation was observable on the higher force levels only. A pair was assigned to the “stable” class, when synchronisation was seen on all force levels (two or three, depending on the MU recruitment level), while “alternating” denoted those pairs that showed occurrence, disappearance and resurgence again of significant synchronisation, or vice versa, on the three force levels respectively. Figure 7 displays two pairs of MUs that are synchronised on all three force levels (“stable”). In example A synchronisation is becoming stronger with force increase, while the opposite is the case for example B; nevertheless both show a “stable” occurrence of synchronisation. According to prediction 1, the majority of the MU pairs (71/93, 76%) was not synchronised on all force levels tested (Table 3). Of these 71 MU pairs, a significant majority fell into the “low” category, indicating a preference for synchronisation at low force levels (46/71, 65%, χ^2-test, $P<0.05$). The strength of synchronisation did not increase systematically with force.

Guided by prediction 2, we also investigated whether the firing rates of the synchronised and non-synchronised MU pairs differed. The MUs in the synchronised intra- and intermuscular pairs fired at the respective force levels on average at a lower rate than non-synchronised ones (ANOVA, linear contrasts according to Scheffé, $P<0.001$, Table 4).

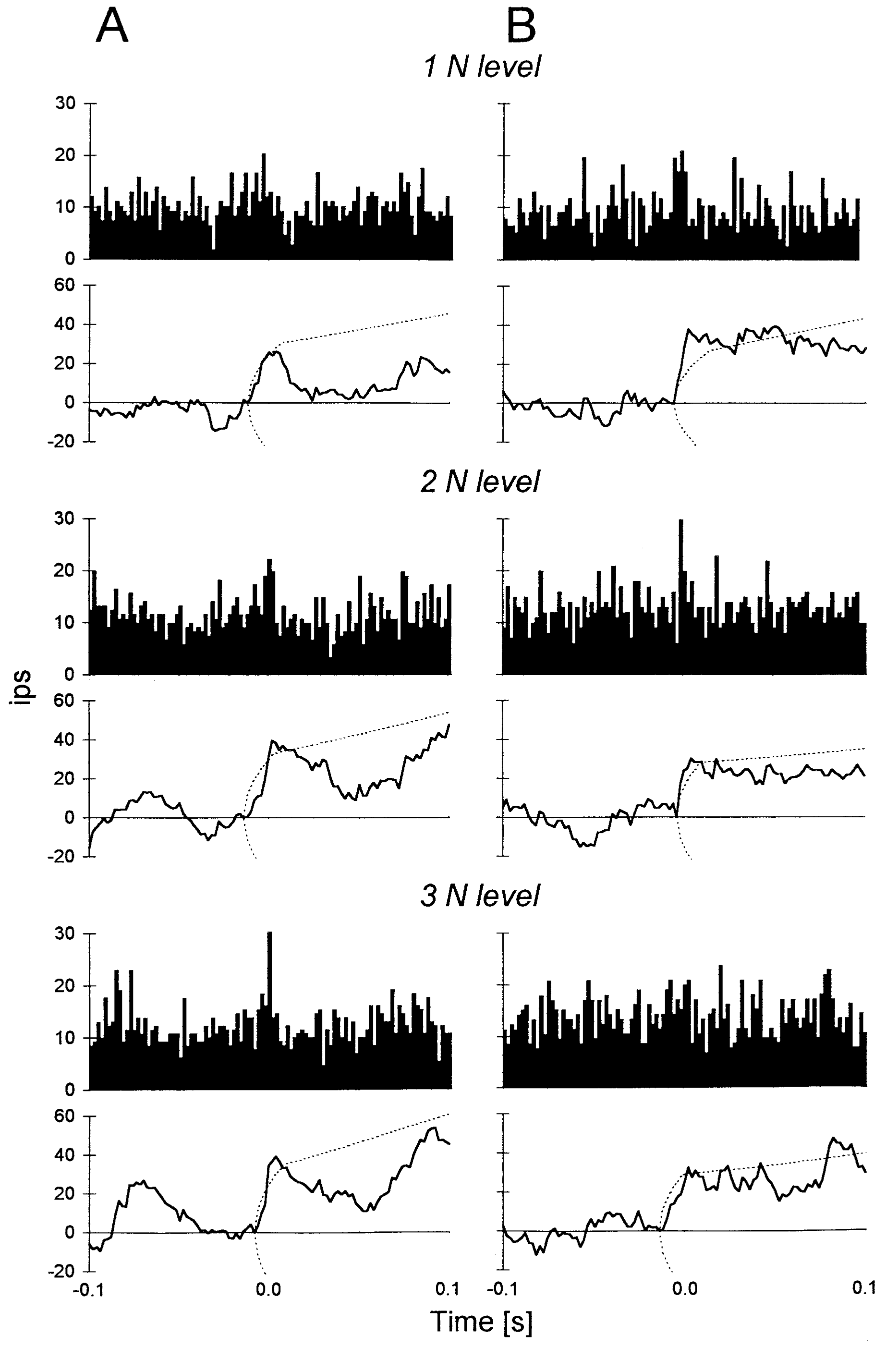
Relationship to multi-unit muscle synergies

As the multi-unit EMG represents the spatial integral of the underlying MU activity, a considerable overlap between the synchronisation at both the multi-unit and sin-

Table 4 Firing frequencies of synchronised and non-synchronised MU pairs (average±standard deviation). The firing frequencies of the synchronised MU pairs are lower than those of the non-synchronised ones (ANOVA, $P<0.001$)

	Force level	Synchronised MU pairs		Non-synchronised MU pairs	
	N	*n*	Firing frequency (Hz)	*n*	Firing frequency (Hz)
Intermuscular	1	26	6.87±1.97	58	7.90±2.48
	2	64	8.14±2.37	150	9.27±2.00
	3	82	9.43±1.77	244	10.10±1.97
Intramuscular	1	26	8.51±0.96	14	9.34±1.18
	2	56	9.45±1.54	38	10.41±1.41
	3	72	10.03±1.96	66	10.92±1.84

Fig. 7A,B Synchronisation of two MU pairs at all three force levels. In **A** the temporal coupling of an *intramuscular* FPL pair increases with force. Synchronisation indices for the three levels: k_{1N} 2.08, k_{2N} 2.02, k_{3N} 2.71. In **B** for an *intermuscular* 1DI/1PI pair the synchronisation is stronger at the lower two force levels. Indices for the three levels: k_{1N} 2.27, k_{2N} 2.34, k_{3N} 1.55



gle MU level was expected. This assumption was tested at each force level separately.

We first compared the temporal coupling of the constituent intermuscular MU pairs with that found for the multi-unit EMG by Maier and Hepp-Reymond (1995b). The first important observation was that temporal coupling at the multi-unit EMG level did not require the synchronisation of the ensemble of underlying MUs. In the 45 muscle pairs displaying significant temporal coupling, only five muscle pairs showed synchronisation for all the discriminated MUs. Nineteen muscle pairs had only partial MU synchronisation. Figure 8 shows an example of an MU pair with synchronisation at the 1 N level only, while the multi-unit EMG from which the MUs were extracted displayed synchrony on all three force levels. Thus, either one MU pair with strong synchronisation or the weaker synchrony of several MU pairs can lead to the short-term temporal coupling detected at the multi-unit EMG level.

We then investigated to what extent MU synchronisation could generally be seen at the multi-unit EMG level. Only 55% of the 86 muscle pairs containing synchronised MUs showed significant synchronisation peaks in the multi-unit EMG. This seems to indicate that

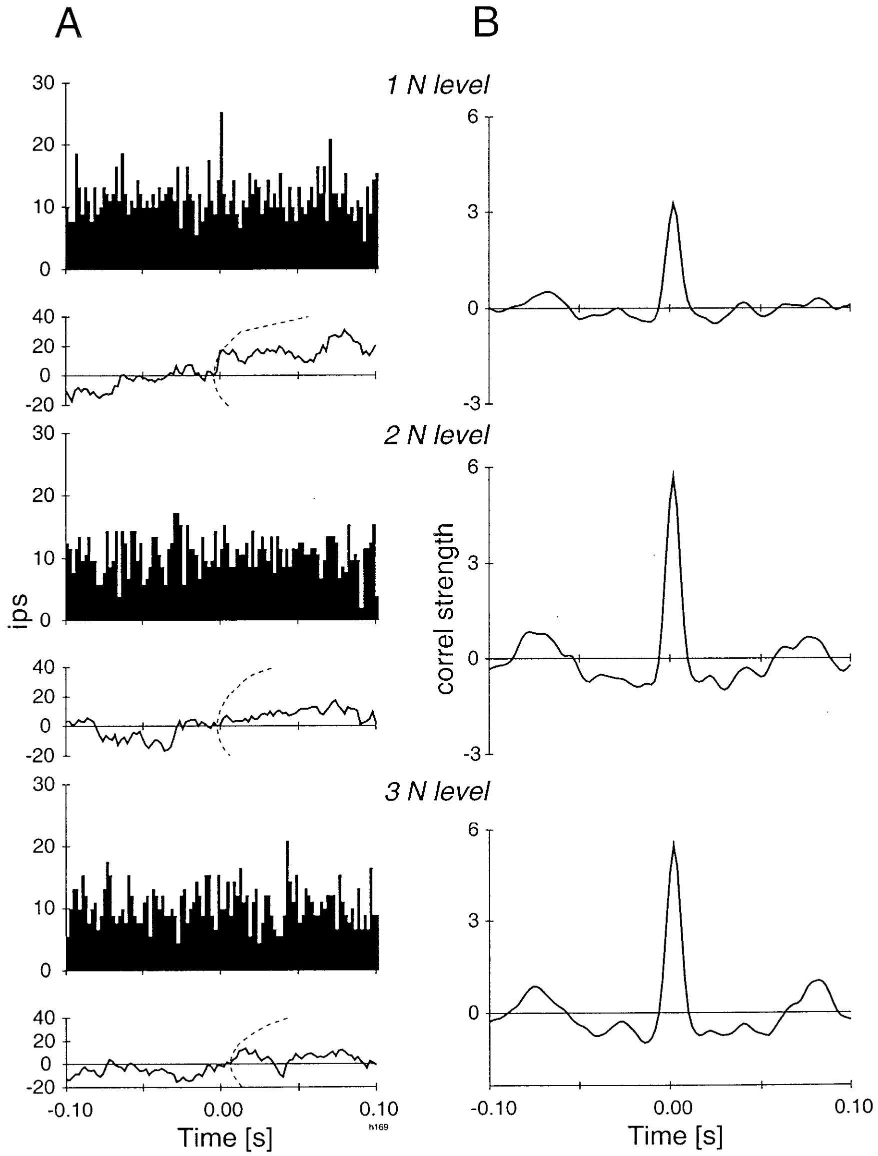


Fig. 8 Comparison of synchronisation at the single unit **(A)** and multi-unit EMG **(B)** level for an FDS-OPP pair. The two MUs used in **A** were extracted from the multi-unit EMG signals of the FDS and OPP muscles, respectively. The synchronisation of the MU pair is only significant at the 1-N level, while multi-unit synchronisation is present at all three levels, reaching a maximum at 2 N

the specific contribution of the synchronised MUs was quite low in comparison to other non-synchronised MUs dominating the integrative EMG signal. A further clear finding was that the synchronisation strength of MU pairs was significantly higher when the multi-unit EMG of both muscles was also synchronised (one-sided *t*-test, $P<0.05$ for index *k*, $P<0.01$ for index *k'*).

Discussion

In the present study we investigated the synchronisation of the MUs of several thumb and index finger muscles participating in the production of force in the precision grip. Temporal coupling of MUs belonging to different motoneuronal pools may be a possible strategy for controlling the intricate and interdependent biomechanical system of the hand (Gielen et al. 1995). Two central issues were addressed: first, the extent to which MU synchronisation occurs in a natural motor behaviour, compared to the rather artificial tasks used by other investigators, and, second, the role of the main task variable, i.e. force, in the occurrence of synchronisation. The influence of MU firing rate and recruitment level on the extent and variability of synchronisation was tested by systematically varying the grip force. Synchronisation was detected in a variety of intra- and intermuscular MU combinations, its occurrence being lower for the latter pairs. The most interesting and new observation was that the recruitment level and the low firing rates at these force levels emerged as favourable factors for the occurrence of synchronisation. This may explain why synchronisation on all three force levels required by the task was so rare, and its strength so variable in comparison to previous studies on MU synchronisation.

Motor unit detection software

Based on the results of the templates, on the interpotential interval histograms and on the rate coding in the motor task (Figs. 1, 2, 3), we are confident that the ARTMUP system (Haas and Meyer 1989) produced valid MU discrimination data. MU potentials could be traced over longer periods of time (20 15-s trials with rest periods of about 10 s between trials), even though the templates had to be regenerated anew for each trial due to limited computer storage capacity. The authors of ARTMUP claimed a 95% discrimination rate of their algorithm with several synthetic benchmark tests (Haas 1989). Our findings based on physiological data yielded 78% with full and 22% with partial discrimination. In partially discriminated segments at least one MU spike was discriminated.

Motor unit behaviour

The vast majority of MUs (77/92) showed a significant positive correlation between their firing rate and the grip force. This speaks in favour of a broad pattern of muscle coactivation in the precision grip, with only a few muscles involved in stiffness or postural control of wrist and/or finger joints. Within individual finger muscles the MU behaviour was not always homogeneous. While a large majority of intrinsic muscles usually contained MUs with highly significant positive correlations between firing rate and force, other MU populations, mainly in extrinsic muscles, displayed weaker correlations with a large variance. In the force range investigated, the MUs of intrinsic muscles also had a considerably higher force sensitivity than those of extrinsic muscles. On the whole, the results obtained on the MU level, namely the more important contribution of the intrinsic finger MUs to the fine regulation of isometric grip force, support the findings of the previous multi-unit analysis (Maier and Hepp-Reymond 1995a). The possible influence of fatigue (Bigland-Ritchie et al. 1986) was controlled and found to be of minor importance. The discharge rate in the 20 consecutive trials of one experimental session significantly increased in 9 of 92 MUs, while insignificant rate change was seen in the majority (67 MUs). In 16 MUs the firing frequency significantly decreased; however, whether this can be attributed to fatigue or a change in strategy remains open.

Motor unit synergy

If muscle synergy is a means for the CNS to coordinate muscle activation, then this should manifest itself in short-term synchronisation within and between the large MU pools during our task which required a high level of muscle coordination. We based our analysis mainly on the occurrence rather than the strength of synchronisation since the commonly used synchronisation indices seem to be frequency dependent (Nordstrom et al. 1992; Matthews 1996). According to Vaughan and Kirkwood (1997), the peak width in cross-correlograms of synchronised MUs can give some indication of the underlying synaptic connectivity. In our findings, the presence of narrow peaks in 50% of the cases – less than 5–6 ms measured at the base of the peak (which compares to approximately 2.5 ms half-width of Vaughan and Kirkwood 1997) – indeed speaks in favour of monosynaptic short-term motoneurone synchrony mediated by last-order branched axons. However, broader intra- and intermuscular peaks also indicate the existence of di- or oligosynaptic divergence at a non-premotoneuronal, probably spinal or even cortical level. It has to be noted, however, that the peak widths we report here are narrower than most of those reported in the literature [e.g. Bremner et al. (1991a) mode 13 ms; Schmied et al. (1994) mean 8.5 ms]. However, Nordstrom et al. (1990) reported 3-ms peak widths for masseter MU pairs. Moreover, our distribution of peak widths is skewed, contrary to most others.

It may be possible that the narrower peaks are due to the low signal-to-noise ratio in our data. We think that the present data set, though based on relatively few triggers, does have a sufficient robustness in terms of occurrence (see “Materials and methods”), but may be at the limits for detecting finer details such as peak width. In particular, two methodological aspects may lead to narrower peaks: the shorter period for calculating the CUSUM baseline, and the criterion of monotonic growth of the CUSUM for establishing the width. These aspects could account for the skewed distribution. However, there was no significant correlation between numbers of spikes and peak width, i.e. within our sample the peak width was independent of the spike count. Nevertheless, consistent with Bremner et al. (1991a), we did not find any difference in peak width for the differently innervated intermuscular MU pairs.

MU synchronisation was found in 78% of intra- and in 45% of intermuscular pairs. These results are, compared to other studies, well within the range for intramuscular pairs but are at the lower boundary for intermuscular ones (Table 5). Several factors may account for the differences with these studies: first, the motor task and the experimental paradigm, second, the feedback condition, third, the firing rates and forces, and, finally, the recruitment level.

First, in most studies the subjects were asked to continuously exert weak torque around one joint over several minutes without modulation of joint torque or MU firing rate. In our paradigm, in contrast, the subjects had to follow a ramp-and-hold force trajectory repeatedly between 0 and 3 N by applying force on a transducer held between thumb and index finger, thereby recruiting the discriminated MUs in each trial. Another non-negligible factor is the type of muscle activation pattern investigated. While in our experimental setup the subjects were asked to exert isometric force in the precision grip, i.e. with a large number of coactive muscles, other investiga-

Table 5 Prevalence of single motor unit synchronisation as described by several authors. This overview shows the wide range of synchronisation in the various studies (*TA* tibialis anterior, *DELT* deltoid muscle, *ECR* extensor carpi radialis, *ECU* extensor carpi ulnaris, *Vis. & aud.* visual and auditory feedback of motor unit, *IAM, IRM* intra- and intermuscular motor unit pair, respectively, *Dom.*,*N-dom.* dominant and non-dominant hand, *intr. & extr.* intrinsic and extrinsic finger muscles)

Authors	Muscles	Degree of synchronisation	Feedback	Firing rate, force	IAM/IRM (*n*)	Comment
Bremner et al. 1991a	1DI, 2DI	67–100%	Vis. & aud.	~10 Hz	IAM	Table 1: class A–C
	4DI, EPB, EDC, FDS	68–77%			IRM	Class D
Datta and Stephens 1990	1DI	88%	Vis. & aud.	~10 Hz	IAM	–
DeLuca and Mambrito 1987	FPL, EPL	Not quantified	Force	<60% MVC	IAM/IRM	–
DeLuca et al. 1993	TA Delt 1DI ECU ECR	54% 45% 71% 74% 69%	Force	30% MVC	IAM	–
Logigian et al. 1988	ECR	68%	Not specified	Not specified	IAM	Tremor
Milner-Brown et al. 1973	1DI	100%	Vis. & aud.	5–10 Hz	IAM	One subject 100%, the other 0%
		0%				
Nordstrom et al. 1992	1DI	–	Vis. & aud.	7.5–17.5 Hz	IAM	–
Schmied et al. 1993	EDC	70%	Vis. & aud.	Regular	IAM	–
Schmied et al. 1994	ECR	88% 69%	Vis. & aud.	Not specified	IAM	Dom. N-dom.
Semmler and Nordstrom 1995	1DI	51% 81%	Vis. & aud.	Constant rate	IAM	Dom. N-dom.
Present study	15 intr. & extr. finger muscles	78%	Force	1, 2, 3 N	IAM	
		45%			IRM	

tors generally restricted their task to isometric contraction of a limited number of synergist muscles at one joint (Bremner et al. 1991a, 1991b, 1991c; Datta and Stephens 1990; Milner-Brown et al. 1973; Nordstrom et al. 1992). Moreover, coactivation of different muscles has rarely been investigated (Bremner et al. 1991a; DeLuca and Mambrito 1987).

Second, the type of feedback signal presented to the subjects during performance of the tasks varied considerably among studies. In the majority of cases, visual and/or auditory feedback of the MU activity was the rule whereas in our experiments only the total exerted grip force was presented to the subjects. Thus, the results in most other studies may have been biased by the feedback of the MU discharge, as demonstrated by Schmied et al. (1993), who showed that the level of synchronisation could voluntarily be changed by giving an appropriate feedback.

Third, the occurrence of short-term synchronisation should statistically increase with increasing discharge rate of the MUs as the cortical drive – a putative main source for synchronisation (Datta et al. 1991; Farmer et al. 1993) – also increases with higher forces (Fetz et al. 1989). Therefore, we expected to find more short-term synchronisation at higher force levels. However, the main present result is that MU synchronisation occurs predominantly at lower force, just at or after recruitment. This suggests that the large number of central and peripheral afferent inputs to the motoneuronal pools at higher force decreases the influence of any particular synchronising presynaptic source; in other words the ratio of synchronising vs non-synchronising input is getting smaller. In particular, the synchronising input delivered by the corticomotoneuronal system may reach the limit of its working range and saturate earlier than other non-synchronising inputs. Indeed, several investigators have already mentioned the higher degree of MU synchronisation at low activation levels (Dietz et al. 1976; Nordstrom et al. 1992; Matthews 1996). Moreover, in the present investigation synchronisation is rarely stable over the whole investigated force range. In fact, synchronous firing on all active force levels occurs in only 7 of 166 inter- and in 15 of 69 intramuscular pairs (Table 3). If synchronisation arises preferentially in the lowest range of the MU firing frequency, then the increase in firing rate with higher forces, due to rate coding, may well be the cause of the less frequent and unstable synchronisation observed at higher forces. Similarly, Schmied et al. (1994) showed that the smaller the difference between MU firing rates the greater the degree of synchronisation. In several of the experiments performed by other groups, the low firing rates required (usually about 10 Hz, i.e. close to recruitment level) may, as our results suggest, be a central factor giving rise to synchronisation.

Finally, the main observation of the present investigation, i.e. the fact that the highest probability of synchronisation occurs just at the force level above recruitment, is in contradiction with DeLuca et al. (1993), who concluded that the MU recruitment threshold had no influence on synchronisation. However, they had tested MU pairs for synchronisation at 30% MVC and not at the level of recruitment as we did. We, in addition, could demonstrate that the difference between the recruitment levels of the two MUs in a pair definitely plays a role in synchronisation. The closer the two levels are, the higher is the probability of synchronising. This may be a reflection of the fact that the contribution of any excitatory postsynaptic potential, whether synchronous or not, to the precise timing of motoneurone firing is strongest close to recruitment threshold. This finding which suggests that MUs with similar force ranges share a common input is in line with Datta and Stephens (1990) who, for 1DI MUs, had come to the conclusion that the synchronisation strength was inversely related to differences in recruitment threshold.

Relationship between temporal coupling of motor units and of multi-unit EMG

The differences between synergistic activation of single MUs in this study and the corresponding multi-unit activity (Maier and Hepp-Reymond 1995b) are to a certain extent due to the selection of MUs. Since our analysis was based on discrete digital data due to the MU discrimination process, we could extract only part of the spectral richness of the multi-unit EMG. Therefore, it is not surprising that the results of the two analyses do not overlap to 100%. The essence of this comparison is that usually only part of the constituent MU population is temporally coupled in an otherwise fully synchronised muscle. At least for intramuscular pairs, this may be surprising in view of the fact that corticomotoneuronal cell axons branch to most if not all motoneurones in a pool (Porter and Lemon 1993). However, since the same pool receives input from many, not necessarily synchronised, corticomotoneuronal cells, as well as asynchronous input from other sources, it seems likely that only parts of the constituent MUs are synchronised. In consequence, depending on the ratio between asynchronous and synchronous contribution of underlying MUs, not every MU synchronisation could be detected at the multi-unit EMG level.

Functional relevance of synchronisation

What is the functional importance of synchronisation? We have shown that synchronisation occurs to various degrees in pairs of MUs of different hand muscles and within the same muscle. However, except for the time of recruitment, where it is most robust, synchronisation is dispersed over time during the task execution in a seemingly sparse and arbitrary manner. It has to be kept in mind that too high a degree of synchronisation in a motoneuronal pool can be detrimental and lead to instability and tremor (Freund 1983; Logigian et al. 1988). In a natural task such as the precision grip, where synchronisation might be used to reduce the complexity of an overdetermined biomechanical system, we expected, if this were the case, to find higher levels of synchrony. Contrary to this expectation, we report, especially in the intermuscular MU pairs, not only less synchronisation but also less stable synchronisation, when compared to tasks with a single degree of freedom and optimised feedback conditions. This result runs counter to the notion that synergy, as expressed in MU synchrony, is a means for the CNS to reduce an excess in degrees of freedom. Two points need to be considered. First, our data indicate that synchrony depends in part on the MU biomechanical properties, as shown in more detail by Schmied et al. (1994). This means that synchrony has a peripheral determinant. Second, the peak widths, although on average smaller than in most other studies, still suggest that inputs of last-order branched axons (narrow peaks) as well as presynaptically synchronised inputs (broader peaks) contribute to overall synchrony. The relative contribution of these processes is unknown. The anatomical last-order branching pattern is task-independent and by necessity produces MU synchrony simply as a by-product of the divergent connections. In contrast, a functional, task-dependent synergy effectively needs to be generated at the presynaptic level, e.g. by the selection of the appropriate corticomotoneuronal pool. Indeed, a 15 to 30 Hz coherence between oscillatory motor cortex activity and EMG has been demonstrated in humans (Conway et al. 1995; Salenius et al. 1996) as well as in monkeys (Baker et al. 1997). This coherence showed a task-dependent modulation and was particularly dominant during steady-state co-contraction in precision grip (Kilner et al. 1999), but was absent during transitions. Compatible with these observations, our data on the instability of synchrony, despite a continuous demand on control and an invariant performance, seem to suggest that non-synchronous means of control exist. Whether one mode of control predominates over the other in particular tasks, or whether they operate concurrently or are mutually exclusive, remains to be determined.

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