Relation between Location of a Motor Unit in the Human Biceps Brachii and Its Critical Firing Levels for Different Tasks

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Critical firing levels (CFLs) of single motor units (MUs) in the long head of the human biceps brachii muscle were determined in combinations of two isometric tasks: flexion of the elbow, supination of the lower arm, and exorotation of the humerus, as well as the corresponding antagonistic tasks. The MU activity was recorded by 25-μm bipolar wire electrodes. Four main patterns of MU recruitment, related to the recording location in the muscle, were found: (i) MUs active only when flexing the elbow were located mostly laterally. (ii) MUs active only when supinating were all located medially. (iii) MUs whose CFL depended on a linear combination of flexion and supination forces were all located medially. Some of these MUs could not be recruited during pronation. (iv) Nonlinearly behaving MUs, located centrally. The relative weights of flexion and supination input were constant for all units, whose CFL depended on a linear sum of flexion and supination forces, as well as for the nonlinearly behaving units. Supination and exorotation showed equivalent CFL changes when they were combined with the flexion task. Extension did not change the CFL for supination- or exorotation tasks. No clear difference was found between the ratios of the peak twitch forces in flexion and supination direction for laterally and medially located small muscle areas or single MUs. A simple model of the motoneuron pool organization is proposed to explain our findings.

INTRODUCTION

Recent studies have shown that in multifunctional muscles the recruitment order of motor units (MUs) depends on the specific task to which that muscle contributes. Investigating pairs of MUs, Thomas et al. (35) found that their subjects could manipulate the recruitment order in the first dorsal interosseus by changing the direction of the task. Desmedt (12, 13) found reversals of recruitment order in that muscle when recording simultaneously at two sites in the muscle. It was found in the human biceps (11, 19) that recruitment of each investigated MU depended either on flexion or on supination and exorotation forces. Also units were found that were recruited when a linear combination of these forces exceeded a certain threshold.

The territory of the muscle fibers of a MU usually occupies only a fraction of the cross-sectional area of the muscle (6, 7, 18, 32), thereby supplying a means for a selective use of parts of the muscle. This seems appropriate for muscles of wide origin like, e.g., m. deltoideus and m. pectoralis, but less for the long head of the human biceps brachii (BLH). In this study we show that task specificity of a MU and location in the human BLH are related.

Motor units recorded in the medial side of the BLH are preferably recruited during isometric supination or exorotation [for a definition of these tasks see ter Haar Romeny et al. (19)], whereas laterally recorded MUs are recruited mainly during isometric flexion, independent of supination or exorotation force. Since medial units are attached to the outside of the insertion area of the tendon on the radius they may have a slightly more favorable lever for supination in the semiprone isometric position in which all experiments were done. Hence we investigated whether or not the site-dependent behavior of MUs was related to peak force of twitches in flexion and supination direction, obtained by spike-triggered averaging or local stimulation of small muscle areas.

Swett et al. (33) found a somatotopic relation between the craniocaudal sequence of motoneurons in the spinal cord and the sites of the muscle units in the medial gastrocnemius of the cat. Similar results were found in the cat's m. peroneus longus (15, 21). Our results are discussed in view of these findings.

METHODS

Experiments were conducted on five normal subjects, aged 27 to 54 years, with no known history of neurological disorder. The methods were similar to those described in detail elsewhere (19). A resume and some modifications are given below.

Three different tasks in which the BLH muscle is involved were investigated: (i) flexion (F)—extension of the elbow joint, (ii) supination (S)—pronation

of the forearm, and (iii) exorotation (E)—endorotation of the humerus. Forces in all directions were measured at the wrist by means of a measuring device, consisting of concentric rings around the wrist, such that forces in flexion-extension, supination–pronation, and endorotation–exorotation could be measured independently by means of strain gauges attached to the connections between the rings.

Electromyogram Recording. Motor unit activity was recorded by means of 25-μm, nylon-coated, fine wire electrodes. All signals were recorded on an instrumentation recorder (Honeywell 101, bandwidth 10 kHz) for further analysis. During the analysis of the data special attention was paid to ensure single-unit recording by constantly monitoring the waveform of each motor unit action potential on a large oscilloscope screen. With these electrodes one to three MU action potentials could be reliably detected per bipolar lead, to 32 Nm flexion [about 45% maximum voluntary contraction (MVC)]. With these high forces there was much background activity, but in most experiments some high-amplitude MU action potentials could be reliably distinguished throughout. About 70% of all electrode pairs gave a stable signal, the others showed movement artifacts (and thus changes of the MU action potential form and amplitude), or were not selective enough, or even showed no signal at all (or a very poor signal to noise ratio). The place of insertion was carefully chosen, just distal to the end-plate area of the right BLH. In six experiments wires were inserted at two places, one laterally and one medially of the center-line of the muscle, as close to the belly's boundary ($\pm$5 mm) as possible. Insertion depth of the needle varied from 2 to 3.5 cm, depending on the thickness of the fatty layers of the arm. The uncertainty about the recording position in the muscle is estimated to be about 0.5 cm. In three experiments a third set of wires was inserted centrally in the muscle between the lateral and medial set.

Tasks. The subject was informed about the force-levels in the three different directions by displaying them on an oscilloscope in front of him on the table. Subjects were instructed to relax their muscles completely between successive experiments. Next the subject was asked to maintain a particular force in a given direction (e.g., supination) at a certain level, keeping the other forces zero. Levels were presented in a random order. As soon as the subject accomplished this task he was asked to increase a force in another prescribed direction (e.g., flexion) slowly. In all experiments only two forces were varied simultaneously while the force in the third direction was kept zero. For each MU the combination of two forces, at which the unit started firing, was determined, i.e., the critical firing level (CFL). Each combination of forces was obtained in two ways by reversing the order of the two tasks. The speed of contraction was determined by the subject and did not show very much variation between subjects and experiments. The average time to contract

from zero to about 50% of the maximal force was about 10 s. Examples of actual recordings are shown in Figs. 1 and 3. Speed of contraction was slow enough to avoid the influence of velocity components (13). Recordings in which irregularities were seen in the speed of contraction were excluded from analysis.
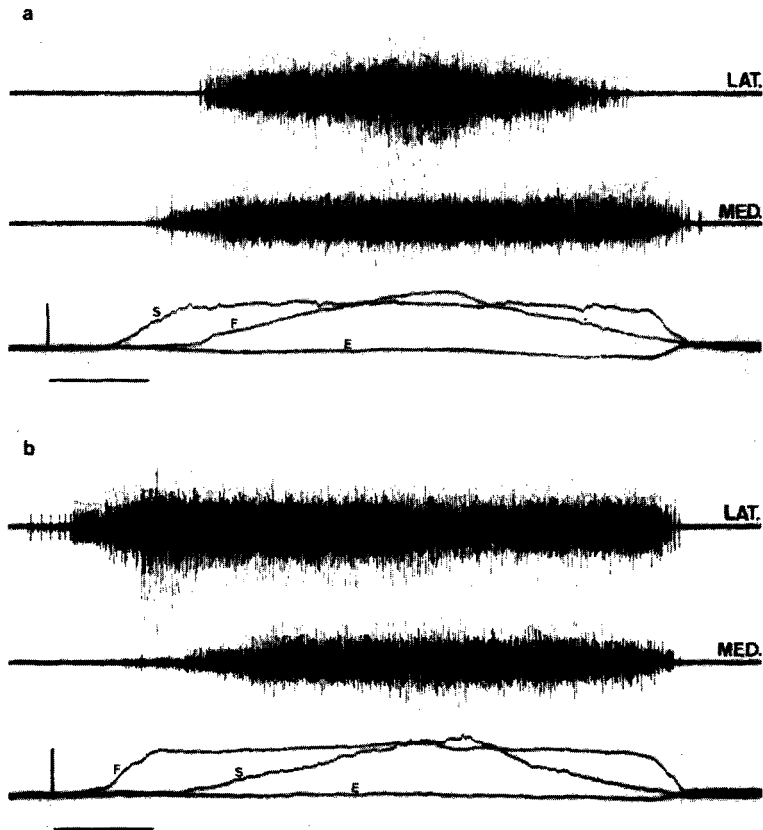

FIG. 1. Myograms from the same experiment. a—Typical experiment. The subject first isometrically supinated to a certain level, then slowly increased isometric flexion force, maintaining the supination force constant. Forces are shown in the lower traces. The exorotation force was zero throughout. Upper trace: bipolar wire EMG recording from a lateral site in the belly of the biceps long head muscle. Middle trace: recording from a medial site in the same muscle. b—Similar experiment, but now the two forces were exerted in reversed order. c—Interchanging flexion and supination. Flexion force was slowly released while supination force slowly increased. Time calibration: 2 s. Forces (torques) in Newton-meters (Nm). Force calibration: 2.7 Nm flexion (F), 0.6 Nm supination (S), 0.6 Nm exorotation (E).
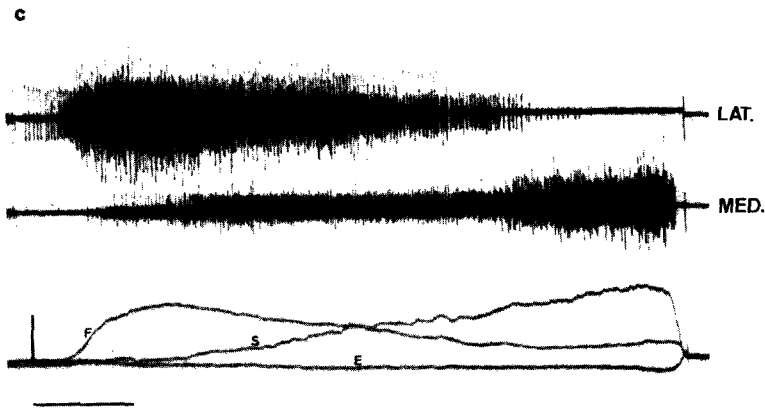
c

FIG. 1—*Continued.*

Determination of Twitch Forces of Small Muscle Areas or Single Motor Units. How the lateral or medial part of the muscle (in which the muscle unit had its territory) contributed to forces in different directions, was measured in two ways:

(i) Stimulating pulses (2 ms duration) were applied to a pair of wire electrodes. By recording from another pair of wire electrodes in the same location in the muscle it could be checked that several muscle fibers in the immediate neighborhood were activated directly (most likely belonging to many different MUs). Increasing the stimulation current through the electrode above a certain level resulted in MU stimulation, characterized by a longer latency of the action potential, probably due to slow axon-collateral conduction. Stimulation was carried out below this level to be certain not to stimulate an unknown muscle area. Stimulation pulses were delivered (randomly alternated) at the lateral and medial sites of the muscle with random intervals ($1000 < \Delta T < 1500$ ms). Twitches were recorded in the three force directions, while the subject isometrically held a prescribed level of force(s).

(ii) The contribution of twitches of only one MU in the different directions were determined by means of spike-triggered averaging. For units with a low twitch force, twitch amplitude in the supination direction usually drowned in the noise. Therefore, reliable twitch shapes could be determined only for MUs with large twitch amplitudes. By means of a microprocessor-based averager, twitches preceded or followed by another twitch of the same MU within 100 ms were excluded from averaging, thereby reducing contamination of the twitch shape and amplitude (26).
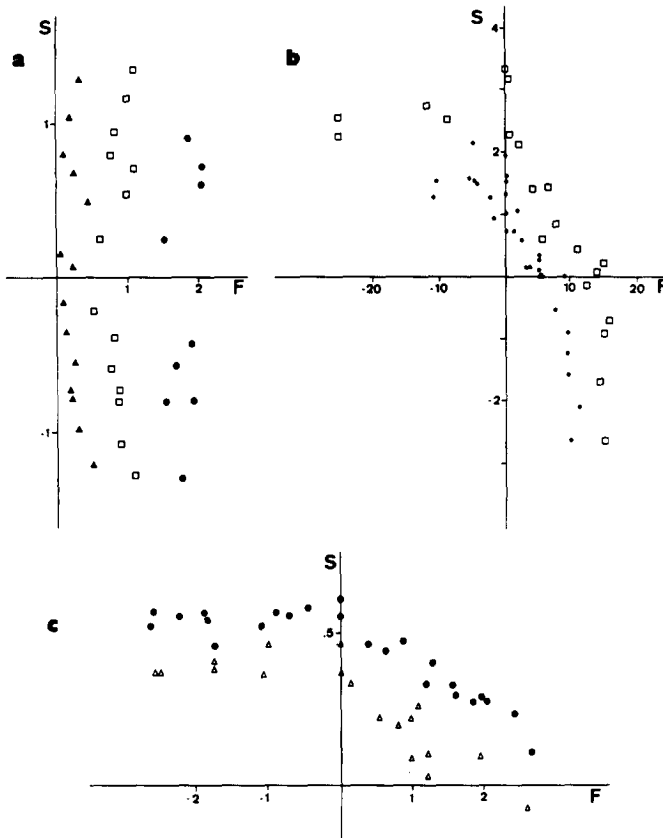
FIG. 2. Critical firing levels (CFLs) for flexion (F) and supination (S) maintaining exorotation zero. Each symbol indicates the combination of forces, at which the motor unit (MU) commenced firing. Different symbols for different MUs. a—"Flexion units," only sensitive for flexion, no matter the level of supination or exorotation; found laterally in the muscle. b—"Summing units," recruited when a linear combination of flexion and supination exceeded a certain threshold; found medially and centrally. All force levels in Newton-meters (Nm). c—"Summing units," inhibited by pronation. Further as b, found only medially. d—"Nonlinear behaving units." CFL for flexion independent of the level of supination, as long as the CFL for supination had not been reached, and vice-versa for supination-flexion. Always high-threshold units (>35% MVC); found centrally. e—"Supination units," only recruited by supination, no matter the level of flexion or extension; found only medially. Exorotation and supination added linearly on these units. Force levels in Nm.

RESULTS

Motor units recorded at different sites in the BLH responded differently on performing the tasks. Results of a typical experiment are shown in Fig. 1a–c. It is seen that when the subject first supinated (Fig. 1a), MUs at the
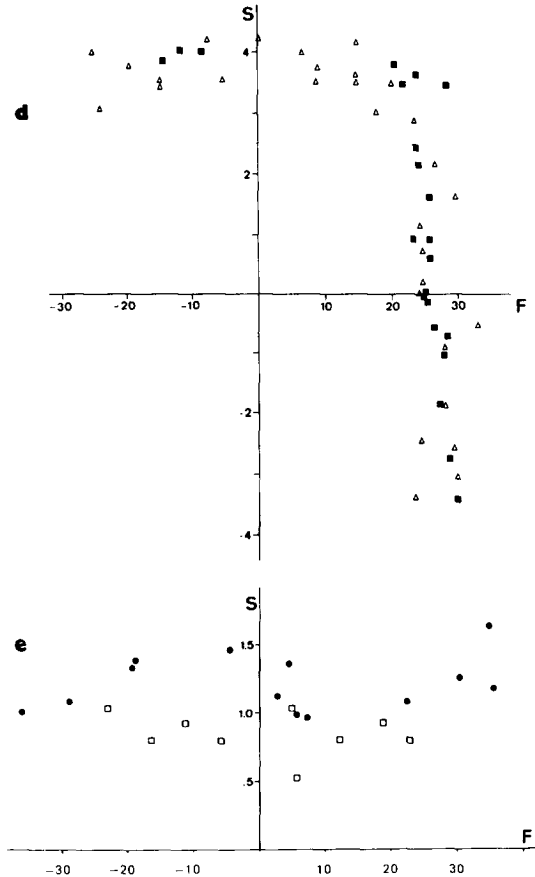
FIG. 2—*Continued.*

medial recording site are recruited first, and reversal of the tasks (Fig. 1b) showed that the laterally recorded MUs were recruited first. Interchanging flexion and supination (Fig. 1c) showed that in this experiment all laterally recorded MU activity was dependent only on force in the flexion direction, whereas activity of medially recorded MUs was dependent on both supination and flexion forces.

Motor unit behavior was characterized by constructing so-called CFL graphs (Fig. 2). In each experiment only two forces were varied, and each point in a CFL graph indicates the levels of the two forces at which the particular MU was recruited. As found before (19), MU activity depended on the specified task. Four main types of CFL graphs were distinguished, corresponding to different MU behavior.

There was relatively little scatter in the recruitment data. Scatter appeared to be primarily related to fluctuations in the maintained forces or in the contraction speed of the slow ramp tasks (14), or by not keeping the third task exactly zero. The CFLs were slightly decreased when the speed of contraction was increased (14).

The influence of the supination (S) task and the exorotation (E) task on the CFL of each recorded MU appeared to be equal when performed simultaneously with the flexion (F) task. Therefore, only the CFL graphs in the F–S plane are shown (Fig. 2). Keeping F zero, the CFL of each MU was always related to a linear sum of S and E forces. None of the MUs found could be recruited by a combination of extension and pronation, extension and endorotation, or pronation and endorotation.

The various types of MU behavior are described below, including where they were found in the muscle. The results are summarized in Table 1.
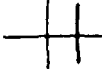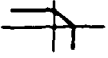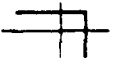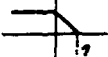
"Flexion Units." Motor units that could be recruited only by exerting force in the flexion direction (19) were recorded at a lateral site in the muscle belly. A preset level of supination or exorotation did not change the CFL for flexion nor did pronation or endorotation (Fig. 2a). These units will be referred to as "flexion units." One such unit was recorded centrally. No such units were recruited in the most lateral part of the muscle when a force in the extension direction was exerted, or when the F force was zero, no matter the level of S or E (see Fig. 3b).

"Supination Units." Units that could be recruited only by a combination of S and E forces, no matter the level of F or extension (19), were exclusively found in recordings from the medial side of the BLH, and will be referred to as "supination units" (Fig. 2e).

"Summing Units." In the central and medial part of the muscle we found MUs with a CFL related to a linear combination of two tasks (19). For example, a certain maintained level of S decreased the apparent threshold for F. These units will be referred to as "summing units." Reversal of the order of the two tasks led to the same CFL graph. When the subject pronated, two different types of behavior were observed: (i) No recruitment when the flexion force was increased during pronation, not even for small pronation forces (see Fig. 2c and compare with b). The recording in Fig. 3a showed that none of the units near the medial electrodes was recruited during increasing flexion forces, except for a unit, situated probably more laterally, which was recruited only during flexion. These units, silent during pronation, were always found medially. (ii) There was recruitment during flexion when the subject pronated, independent of the level of pronation and every time at the same F force (see Fig. 2b). Sometimes the level of F force at which the unit was recruited increased slightly with the increasing pronation level, but always a distinct change of slope was observed in the graph of the CFLs

TABLE 1

Frequency of Motor Units Found According to Recording Position in the Muscle and Function (Critical Firing Level (CFL) Graph)[a]

CFL schematic	Long head		
	Lateral	Central	Medial
(schematic)	12	1	0
(schematic)	0	5	3
(schematic)	0	0	4
(schematic)	0	0	5
(schematic)	0	3	0
(schematic)	0	2	3
(schematic)	0	4	4

[a] The lower two rows show motor units whose CFL graphs could not be determined completely, or where after the experiment it appeared the forces were not exerted to a sufficiently high level to discriminate between nonlinear behavior and "supination units."

when crossing an (co-)ordinate axis. In these graphs horizontal and vertical lines in the second and fourth quadrant, respectively, were always at a level where the axis was intersected by the line in the first quadrant.

Positive Slope. Only one MU, located laterally, showed a flexion–supination CFL graph with a positive slope as was reported elsewhere (19). No systematic search was made for those units, which always had a low F threshold. In this research mainly units with high recruitment thresholds in the flexion direction were examined.

Slopes of Graphs of Critical Firing Levels. We investigated whether or not the slopes of the CFL graphs of the so-called "summing" units, i.e., the ratio of the respective contributions of the two forces, was dependent on the force thresholds. The intercepts of the F and S coordinate axes have been given
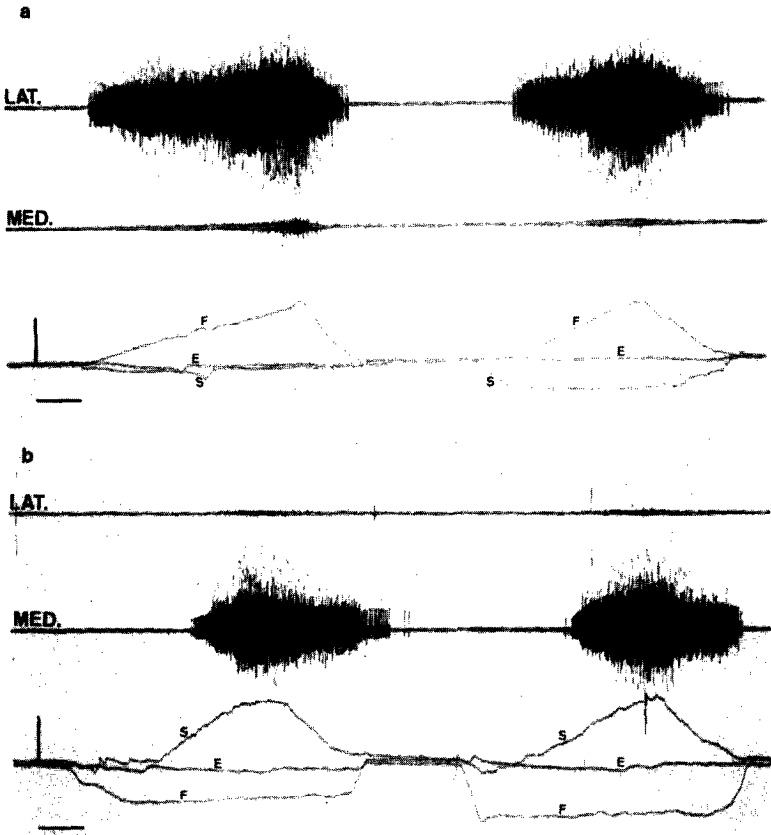
FIG. 3. Myograms of typical experiments. a—With flexion and pronation tasks. Even the slightest level of pronation prevented the MUs in the medial recording in the BLH muscle from firing. b—With supination and extension tasks. Same subject and electrode positions as in a. Time calibration: 2 s. Force calibration: 2.7 Nm flexion, 0.6 Nm supination, 0.6 Nm exorotation.

for all these units in Fig. 4. The results from all subjects were pooled. These units were found centrally and medially. Note that all ratios of F and S forces were approximately equal and were structured on a straight line, meaning that the slopes of the CFL graphs were approximately equal. No apparent relation between the exact location in the muscle and the slope was found.

To determine whether or not the slope was dependent on the angle of the elbow, and thus the length of the BLH, the slope was determined for three units with the elbow angle at 70 and 110 deg. These angles were chosen symmetrically about 90 deg., to prevent any influence of an oblique angle of the moment arm of the biceps tendon on the radius. By continuously
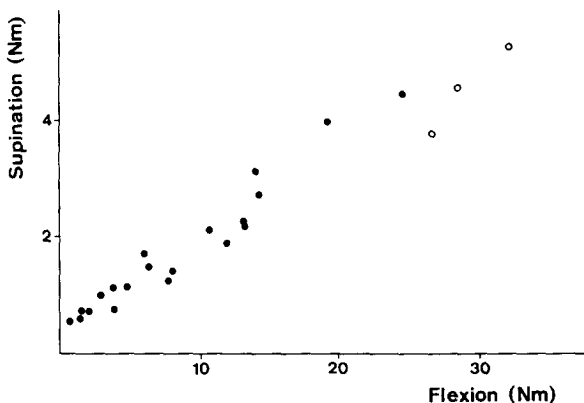
FIG. 4. Intercepts of the flexion and supination coordinate axes of the CFL graphs of all summing units (cf. Fig. 2b, c) solid symbols: Summing units. Open symbols: Nonlinear units (cf. Fig. 2d). For all investigated MUs the relative weighting factor of flexion and supination input appeared to be equal, even for the nonlinear units. The flexion force covered a range to about 45% maximum voluntary contraction. MUs were pooled from all experiments from all subjects.

monitoring the shape of the MU action potential when changing the elbow angle to the new position it was checked that it was the same MU that kept firing. The slope was equal for both elbow angles for the units studied (see Fig. 5).

"Nonlinear Behaving Units." Some units that initially seemed to be activated for one task proved to be also dependent on another task only provided the input was large enough. An example of such a unit is shown in Fig. 2d. It was carefully checked that it was the same unit that was recruited each time. These MUs were found centrally in the BLH. In the CFL graph a clear angle of 90 deg. was observed. All these units showed the same behavior in the second and fourth quadrant. A remarkable finding was that the intercepts of the coordinate axes, when plotted in Fig. 4, did fit very well (open data points) to the data of the "summing units." All these units demonstrated high thresholds, i.e., were recruited only after exerting F forces of more than 26 Nm. Units that showed this behavior for the F–S task combination, did likewise for F–E. Again, scatter was relatively small. For one MU the 90 deg. angle as seen in Fig. 2d was rounded a little, but the CFL graph was definitely different from a "summing unit." The units as displayed in Fig. 2a and e were sensitive for one force only in the range of forces measured, this range well exceeding the ratio as given by the data in Fig. 4.

Test for Functional Significance of the Relation between Task Specificity and Location in the Muscle. The ratio between amplitudes of twitch forces in supination and flexion direction might be different for units at the medial
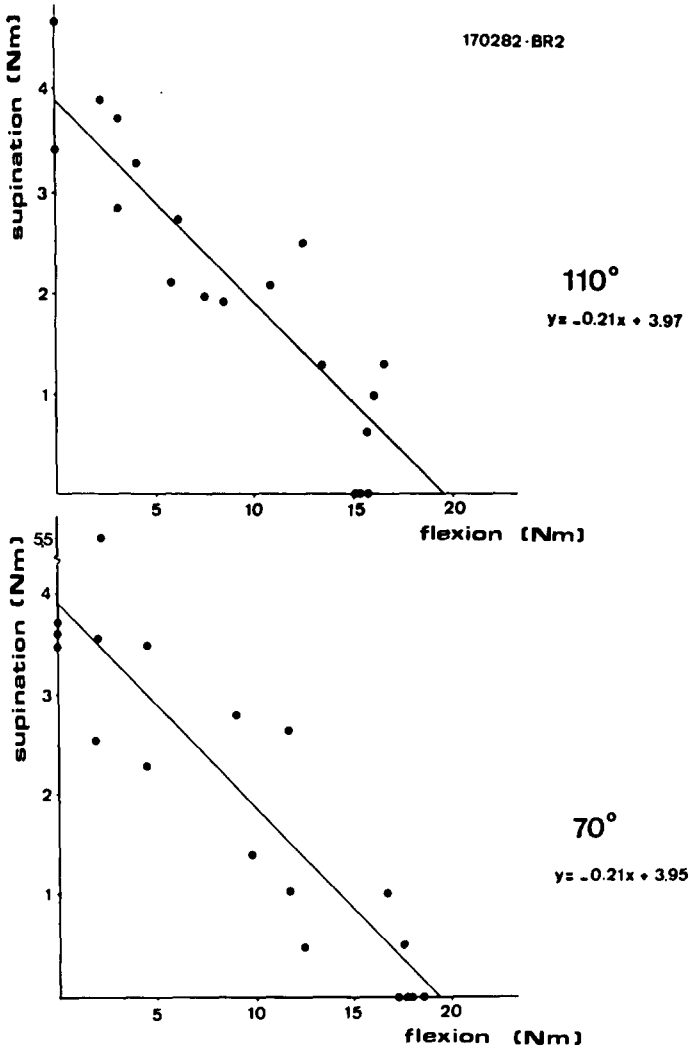
FIG. 5. CFL graph of a MU when the tasks flexion and supination were performed isometrically at two different elbow angles. Upper graph—elbow angle 110 deg, lower graph—elbow angle 70 deg. (Extension corresponds to 180 deg.)

and lateral side of the BLH. This was tested by means of electrical stimulation of small parts of the muscle by means of wire electrodes at the medial and lateral sides of the BLH muscle. Secondly, twitch forces of single (high-threshold) MUs in the F and S direction were determined at the two locations by means of spike-triggered averaging (see Methods). On the surface of the

muscle belly and the distal tendon, different contractions of the muscle were seen and felt when stimulating at these different locations with a somewhat stronger stimulus. This was always a proof that the wire electrodes were placed in the correct muscle at a correct position. The determination of twitch forces of a single MU was possible only for the MUs with high thresholds due to the recording of F and S forces at the wrist and the mechanical damping by the forearm. Contraction times in the F direction were short, 30 to 40 ms, in the S direction a little longer, 35 to 45 ms. Twitch forces in the F direction were between 3 to 14 mNm, and 1 to 3 mNm in the S direction (see Fig. 6).

The ratio of F–S peak twitch forces at the two sites is a measure of the relative contribution of that part of the muscle to the two tasks, and is given in Table 2. Stimulation was carried out while different combinations of F and S forces were exerted. Table 2 reveals that a clear difference in contributions to force in different directions for laterally and medially situated muscle areas or MUs was absent.

DISCUSSION

In this study we showed that MUs with their muscle units in different parts of the BLH muscle are activated selectively according to the task required. We found that at the most lateral side of the muscle, units were recorded
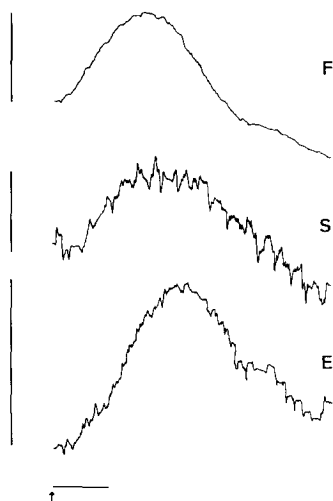

FIG. 6. Twitches recorded simultaneously in the flexion (F), supination (S), and exorotation (E) directions by means of spike-triggered-averaging of a spontaneously firing MU. Average of 1135 discharges. Arrow: time of spike. Calibration: F, 6.5 mNm; S, 1.2 mNm; E, 3.8 mNm. Time calibration: 20 ms.

TABLE 2

Ratios of the Peak Twitch Forces Recorded Simultaneously in the Three Directions[a]

| | Medially | | | Laterally | | At flexion force (Nm) | At supination force (Nm) |
	F/S	S/E	E/F	F/S	S/E	E/F		
	3.5	0.36	0.77	4.2	0.36	0.67	0.0	0.0
	4.7	0.32	0.67	5.0	0.48	0.42	0.0	0.0
	3.5	0.71	0.38	4.6	0.83	0.26	2.8	0.0
	3.1	0.77	0.43	3.3	0.67	0.48	4.8	0.0
	4.1	0.63	0.38	9.2	0.63	0.17	0.0	0.27
	3.5	0.77	0.37	8.0	0.71	0.18	0.0	0.41
	3.9	0.91	0.27	5.1	0.67	0.30	2.8	0.27
	4.1	0.83	0.28	8.5	0.67	0.18	5.0	0.5
	13.1	0.13	0.57	14.4	0.12	0.57	0.0	0.0
	11.3	0.18	0.50	11.0	0.19	0.50	0.0	0.0
	6.5	0.31	0.49	5.8	0.42	0.42	3.4	0.0
	5.0	0.56	0.36	5.0	0.63	0.31	6.7	0.0
	7.0	0.52	0.28	6.4	0.46	0.34	0.0	0.53
	7.1	0.46	0.31	6.9	0.45	0.32	0.0	1.06
	4.5	0.85	0.26	4.4	0.99	0.23	3.4	0.53
	4.3	0.74	0.32	4.1	0.86	0.28	6.7	0.53
	5.0	0.76	0.27	4.8	0.73	0.29	3.4	1.06
	4.3	0.89	0.26	4.6	0.97	0.25	6.7	1.06
$\bar{x}$	5.47	0.50	0.40	6.41	0.60	0.34		
SD	2.73	0.25	0.15	2.86	0.24	0.14		

[a] F—Flexion, S—Supination, E—Exorotation.

that were active only when the task flexion was performed, no matter the level of force in other directions. However, in the central part of the muscle belly only units that could be recruited by a linear combination of the tasks were found. These units were also recorded at medial electrode positions, see Table 1. The MUs recruited only during supination and/or exorotation, no matter the flexion level, were found only in the medial part of the BLH muscle. Different behavior of these groups is seen clearly in Fig. 1c, where flexion and supination were interchanged.

Surprisingly, when a unit could be recruited by the combined inputs of flexion and supination, the relative weight of the inputs on all these moto-neurons was constant and independent of the CFL for pure flexion force. This was true for the whole range of MUs studied, to about 45% of maximum voluntary contraction (=32 Nm flexion). The fact that we did not find a

gradual decrease of the flexion input and a subsequent increase in supination input when recording from lateral to medial locations in the muscle was rather unexpected. This means that the task-dependent behavior of MUs in this muscle is divided in distinct classes. It seems that in such a subset MUs with different CFLs receive a homogeneous input. As stated by Henneman *et al.* (20): "A particular cell receives the same proportion of the total input from each of the systems which is afferent to it." de Luca (25) recorded firing rates of as much as eight concurrently active MUs at one locus in the human deltoid muscle and first dorsal interosseus. He found highly significant correlations between the firing rate fluctuations of these motor units, suggesting a common synaptic input to the motoneurons. However, Person [(28), Fig. 4] found in the human rectus femoris independent behavior of motoneurons in some of his experiments. This finding may suggest that in one muscle, different subsets that may receive independent synaptic input [see discussion also by Clamann (9)] may exist. Wyman *et al.* (37) discuss the possibility that "size principle may hold for motoneurons in a single ventral rootlet (of cat medial gastrocnemius) whose somas are anatomical neighbors (even though they innervate different muscles), but not for motoneurons that are anatomically distant in the cord (even though they innervate the same muscle)."

The ability of the central nervous system to activate different parts of the BLH does not correspond to the rather limited possibilities of the BLH to have different parts of the muscle exerting forces in different directions (Table 1). The human BLH muscle has a rather narrow tendon at origin as well as at insertion. Our findings may be explained by a somatotopic projection of spinal motoneurons to muscle unit territories. Swett *et al.* (33) showed in the cat's medial gastrocnemius a fairly clear craniocaudal organization of the motor outflow to the muscle from lateral to medial. This was later confirmed by Burke *et al.* (7). Also in cat's m. peroneus longus a similar somatotopic relation was found (15, 21). In this muscle the craniocaudal motoneurons projected to anterior–posterior situated muscle fibers. Similar findings were described for tibialis anterior by Basmajian (3).

The findings in these studies suggest that such a relation might also exist for the human BLH. Close synergists usually have strongly overlapping motoneuron columns in the spinal cord [(7, 29) for cat; (30) for terrapin]. It was shown in the squirrel monkey (24) that the positions of medial gastrocnemius, lateral gastrocnemius, and soleus motor nuclei, both relative to each other and relative to the whole triceps surae distribution, were constant from animal to animal. This was so even though the rostrocaudal position of any one of these nuclei appeared to vary as much as one whole segment (4 to 5 mm) as determined by dorsal root entry zone borders. In man the motor nuclei of the BLH and supinator share the same ventral roots and are situated at C5–C6, the BSH a little more rostrally (23). There may be a slightly more

caudal location of the supinator pool than for the BLH pool due to the more distal position of the supinator in the arm. A ventral–dorsal somatotopy is also known to exist in man for extensors–flexors (8).

When a MU can be recruited by more tasks, the synaptic inputs appear to summate linearly, with the same relative weight for all units. It is possible that the algebraic summation of inputs takes place on the motoneuron itself. In the case where nonlinear behavior was found (Fig. 2d) the underlying processes are less clear. Interneurons may play an important as yet unknown role.

Isometric extension appeared to have no influence on the CFL of all the MUs studied. The supination force at which "summing units" were recruited at different levels of maintained extension was independent of the level of extension. This means that there is under these circumstances no indication of reciprocal inhibition on these motoneurons by extensor afferent inputs. If increasing levels of extension should increase the amount of reciprocal inhibition on the "summing unit," one would expect the amount of S input needed to recruit the MU to be gradually increased with increasing extension. This was not the case. However, the possibility is not excluded that this inhibition may take place on units active only during flexion (Fig. 2a). Reciprocal inhibition in man has been a subject of much controversy, but is recently shown in ankle muscles (22, 34). Indications for a strong (reciprocal?) inhibition by the pronator are shown in the medial units whose CFL is displayed in Fig. 2c. Even the slightest level of pronation prevented these units from firing. (Fig. 3a.) It is interesting that also MUs that probably received no inhibitory influence from the pronator were found, as is seen in Fig. 2b. If the inhibition on the BLH motoneuron was directly related to the level of pronation it was expected that higher levels of pronation should require higher flexion force levels to attain the CFL. This, however, was not the case. The CFLs in the fourth quadrant showed a vertical line, indicating no pronation influence. [In some units, behaving as in Fig. 2b, a slight deviation from vertical (negative slope) was detected in the fourth quadrant.] The finding that even slight levels of pronation completely suppress the flexion input on a motoneuron might be explained by a "gating" of the flexion input by pronation, leading to this nonlinear behavior.

A number of investigators have emphasized the inhibitory role of pronation on the biceps (1, 2, 4, 10, 31, 36). This study shows that it is an all or nothing behavior, exerted on only a fraction of the motoneuron pool of the (human) BLH muscle. Bankov and Jørgensen (1) found that the integrated (surface) EMG from the biceps when the forearm was pronated amounted to about 50% of that obtained when the forearm was supinated, indicating that not all MUs of the biceps were inhibited by pronating. The maximum flexion strength of the elbow diminishes to 85% when pronating. This may be due

to the fact that the brachialis is the flexor "par excellence" (2, 5), not the biceps.

The following hypothesis concerning the different synaptic input for different classes of motoneurons of the BLH may be postulated (see Fig. 7): The (supraspinal) flexion input activates the motoneuron pool only partly as does the supination input, with an overlap as indicated in Fig. 7. Lateral units receive only flexion input and cannot be modulated by supination signals. When flexion and supination (or exorotation, see Results) project simultaneously on one neuron, they add linearly. Medial units only receive supination input. There is no reciprocal inhibitory input from the triceps to motoneurons in the BLH that also receive supination input. Pronation may
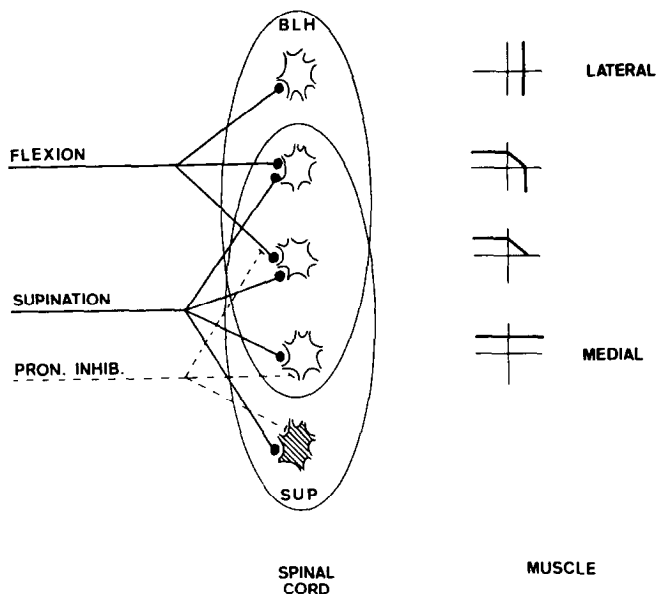

Fig. 7. Somatotopic model to explain the different synaptic inputs to the different MU subsets as found in this study. BLH—biceps long head motoneuron pool in the spinal cord. SUP—supinator motoneuron pool, situated a little more caudally, but overlapping with the BLH. In the BLH area only motoneuronal somata of the BLH are shown; the lower supinator motoneuron is shaded. Flexion (F) synaptic inputs extended to only a fraction of the BLH motoneuron pool, as did supination (S). On the right side of each BLH motoneuron its CFL graph is indicated, also the position in the muscle where it is most likely to record these units. Exorotation (E) inputs were exactly similar to S inputs, on the understanding that when both those inputs act together on one neuron, they add linearly. For clarity E synaptic inputs are not shown. There was no reciprocal inhibitory influence from the extensors on the S input of summing units. There was a "gating" reciprocal inhibition from the pronator to some S recruitable units (see also Discussion).

selectively suppress flexion input on "summing" cells that are silent during pronation [cf. Figs. 3a and 1a (med.)]. Integration of the selective activation of different parts of the motoneuron pool takes place by the overlap of MU territories in the muscle. Eckmiller (17) found a similar subdivision in the motoneuron pool of eye muscles, when eliciting eye movements by a visual or vestibular input in Java monkeys. In conclusion, the location-dependent behavior of muscle units during isometric contractions in different directions is compatible with the paradigm for central nervous system representations of ordered MUs in overlapping loci.

It is clear that this paradigm lacks refinement, for nothing can be said about the undoubtedly important role of interneurons in diverging and converging supraspinal inputs to the neurons in the pool. A very important question is to what extent synergists are activated by heteronymous afferents (whether or not via interneurons?). The fact that the relative contribution of the muscles in the group depends on the combination of tasks (2, 10), and that many synergists are called for assistance only when load or velocity require an increase of force, indicates that convergence of inputs must be at a higher level then the motoneuron itself [see also (16, 27)].

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