J. Physiol. (1985), **359**, *pp.* 107–118
With 4 *text-figures*
Printed in Great Britain

BEHAVIOUR OF MOTOR UNITS OF HUMAN ARM MUSCLES: DIFFERENCES BETWEEN SLOW ISOMETRIC CONTRACTION AND RELAXATION

BY J. J. DENIER VAN DER GON, B. M. TER HAAR ROMENY AND E. J. VAN ZUYLEN*

From the Department of Medical and Physiological Physics, State University of Utrecht, Princetonplein 5, P.O. Box 80.000, 3508 TA Utrecht, The Netherlands

(*Received 9 March 1984*)

SUMMARY

1. The behaviour of motor units in the m. biceps brachii (long head), in the m. brachialis and in the m. supinator during slow isometric contraction and relaxation was studied when subjects were performing different motor tasks. These tasks were: flexion of the elbow joint, supination of the forearm and exorotation of the humerus. Motor unit activity was recorded by means of bipolar fine wire electrodes. In the long head of the biceps, motor unit activity was recorded at medial, central and lateral sites.

2. When the subject relaxed from flexion, the firing rate of motor units located in the biceps and the brachialis was always found to be lower than that at the corresponding level of flexion force during contraction. The firing rate during relaxation decreased slowly and almost linearly with force. However, during relaxation from supination or exorotation, the firing rate of motor units at medial and central locations in the biceps was more or less constant until decruitment. The firing rate of motor units of the supinator during relaxation from supination decreased slowly and was lower than during contraction.

3. Motor units located medially and centrally in the biceps had decruitment thresholds for flexion that were lower than their recruitment thresholds. Motor units on the lateral side of the biceps did not show such a difference. In the brachialis decruitment thresholds for flexion were usually higher than the recruitment thresholds. Differences between decruitment and recruitment thresholds for motor units in the biceps were much more pronounced for supination and exorotation than for flexion. For motor units in the supinator the decruitment threshold during relaxation from supination was higher than the recruitment threshold.

4. The time that had passed after the onset of firing of a motor unit did not influence its decruitment threshold. If, after complete relaxation, the exerted force was increased again, it appeared that the recruitment threshold was changed. It took about 4 s to reach the original recruitment threshold.

5. It is concluded that the relation between the firing rate of a motor unit and total

The authors' names are in alphabetical order. * To whom correspondence should be addressed.

exerted force depends on the phase of contraction. This relation varies within a muscle and between muscles. Furthermore, the results indicate an interchange of activity within the motoneurone pools of the synergists involved in isometrical motor tasks.

INTRODUCTION

It has recently been demonstrated that during slow isometric voluntary relaxations the force level at which a particular motor unit stops firing (decruits) may be different from the force level at which the firing starts during contraction. In the human biceps (long head) most motor units decruit at relatively lower force levels (ter Haar Romeny, Denier van der Gon & Gielen, 1982). This implies that in this muscle at a certain force level more motor units are active during slow relaxation than during slow contraction. Also, during relaxation the firing rates of motor units were often found to be lower than during contraction at the same force level.

In the literature, differences in the force thresholds for recruitment and decruitment of motor units have also been reported or can be seen by careful examination of electromyogram (e.m.g.) recordings for other muscles (De Luca, Lefever, McCue & Xenakis, 1982: first dorsal interosseus and deltoid; Millner-Brown, Stein & Yemm, 1973: first dorsal interosseus; Person & Kudina, 1972: rectus femoris; Desmedt, 1981: first dorsal interosseus). Possible explanations for the change in threshold and the observed relation between force and firing rates of motor units are sometimes included in these reports. Fatigue, potentiation or non-linear summation of twitches and time lags between firing rate and resulting force are supposed to play a role. Fatigue of muscle units may explain why, when force has been exerted for some time, in the biceps more motor units have to be active during relaxation in order to generate the same force. Potentiation and other non-linearities might obscure the relation between firing rate and exerted force and might cause an increased force output of motor units at relatively lower firing rates (Burke, Rudomin & Zajac, 1976).

Finally, it is possible that the relative contribution of (parts of) muscles varies during the different stages of performing a task. An interchange of activity between two anatomical synergists has been reported by O'Donovan, Pinter, Dum & Burke (1982). In that case, motor units that decruit at a higher force level than the level at which they were recruited should be present.

In this study, we describe experiments that were done in order to evaluate the relation between total exerted forces, firing rates and recruitment and decruitment thresholds of motor units and to discriminate between the suggested explanations. The behaviour of motor units of the brachialis and the supinator together with the behaviour of motor units located at different sites in the long head of the biceps (medial, central and lateral) were examined simultaneously. These experiments were carried out for three different isometric motor tasks in which the biceps is involved (flexion, supination and exorotation).

METHODS

The subject was seated with his right arm abducted in a horizontal plane, with the elbow flexed at about 110 deg (full extension = 180 deg). The wrist was fixed tightly in a semiprone position in a force-measuring device. Isometric force in three directions could be measured by means of strain gauges: flexion of the elbow, supination of the forearm and exorotation of the humerus (lifting the wrist upwards). Motor unit activity was recorded with the help of bipolar wire electrodes (diameter 25 μm; material: Karma; Californian Fine Wire Co.), inserted by means of a hollow needle. The recorded signals were filtered (bandpass: 320 Hz–32 kHz). Most recordings were obtained from motor units in the biceps and the brachialis. In one experiment, the activity of motor units in the supinator was recorded. In a few cases, motor unit activity was also recorded in the lateral head of the triceps. The wires (typically four per insertion) were inserted at a short distance (about 2 cm) from the end-plate area of the muscle. In the biceps three different locations were examined simultaneously. The needles were inserted to a depth of about 1·5 cm at medial (number of investigated units: $n = 8$), central ($n = 6$) and lateral ($n = 7$) sites of this muscle. In the brachialis ($n = 9$) only lateral locations were investigated. By electrical stimulation it could be verified that the electrodes had indeed been inserted at the intended locations. The precise location of the recorded motor units in the supinator ($n = 4$) could not be established. Forces and e.m.g. signals were recorded with an analog instrumentation recorder (Honeywell 101, band width: d.c. −10 kHz).

Measurements were performed on five normal subjects (aged 24–55), who gave informed consent. The forces exerted were shown to the subject with the help of an oscilloscope in front of him. By means of a microprocessor system (Motorola M6809) also the optional rate of force increase or decrease was presented on the screen of this oscilloscope. The subject was instructed to increase the exerted force in a certain prescribed direction according to this required force pattern, keeping forces in other directions at zero. To prevent phasic recruitment from interfering with the tonic recruitment order (Grimby & Hannerz, 1973) only slow ramp contractions were performed. In the flexion direction, the contraction and relaxation rates were standardized at about 1 N m/s, for supination at about 0·2 N m/s and for exorotation at about 0·5 N m/s. We confirmed that these contraction rates were not critical for the results of the experiments.

The firing rate and the thresholds of a motor unit were measured during off-line analysis. We took great care that the same unit was studied during the whole experiment. This was achieved by continuously monitoring the wave forms of the units under study at a fast sweep speed, by using a window trigger, a delay line and a large-screen oscilloscope. To determine the firing rate of a motor unit, a microprocessor calculated the reciprocal value of the instantaneous interval between subsequent motor unit action potentials. The firing frequency signal was low-pass filtered (3 Hz) and plotted by means of an $X-Y$ recorder as a function of the exerted force. In this way it was possible to show in one plot the recruitment and decruitment thresholds and the firing behaviour of the motor unit at the corresponding force levels in the contraction and relaxation phase.

RESULTS

Fig. 1*A* shows the firing pattern of a motor unit located medially in the biceps during slow contraction and relaxation of a force exerted in flexion direction according to a prescribed ramp pattern. Meanwhile, the subject had to keep the forces in supination and exorotation direction at zero. It can be seen here that decruitment occurs at a level of flexion force that is lower than its recruitment threshold. In Fig. 1*B* the instantaneous firing rate is shown for the same unit as a function of exerted (flexion) force. This unit recruits at about 4·5 N m flexion force and decruits at about 1·0 N m. The firing rate reaches a value of about 15 Hz and subsequently decreases slowly even with increasing force. This slowly decreasing firing rate was not typical for all motor units. A constant or slightly increasing firing rate with increasing force was usually observed. These relatively small changes in firing rate are consistent with the findings of Kukulka & Clamann (1981) who showed that the force exerted by the biceps brachii is regulated mainly by recruitment and not by modulation of firing rate.

When the exerted flexion force decreased, the firing rate of the motor units always decreased slowly and remained below the values obtained at corresponding force levels during contraction (see, e.g. Fig. 1 *B*). The recordings of the firing behaviour of motor units were reproducible. Variations in the thresholds usually did not exceed 10%. It should be stressed that when a considerably higher (×3) or a much lower ($\frac{1}{5}$) contraction and relaxation rate was used the same firing pattern emerged.

Several aspects of the above-mentioned phenomena were examined in more detail.

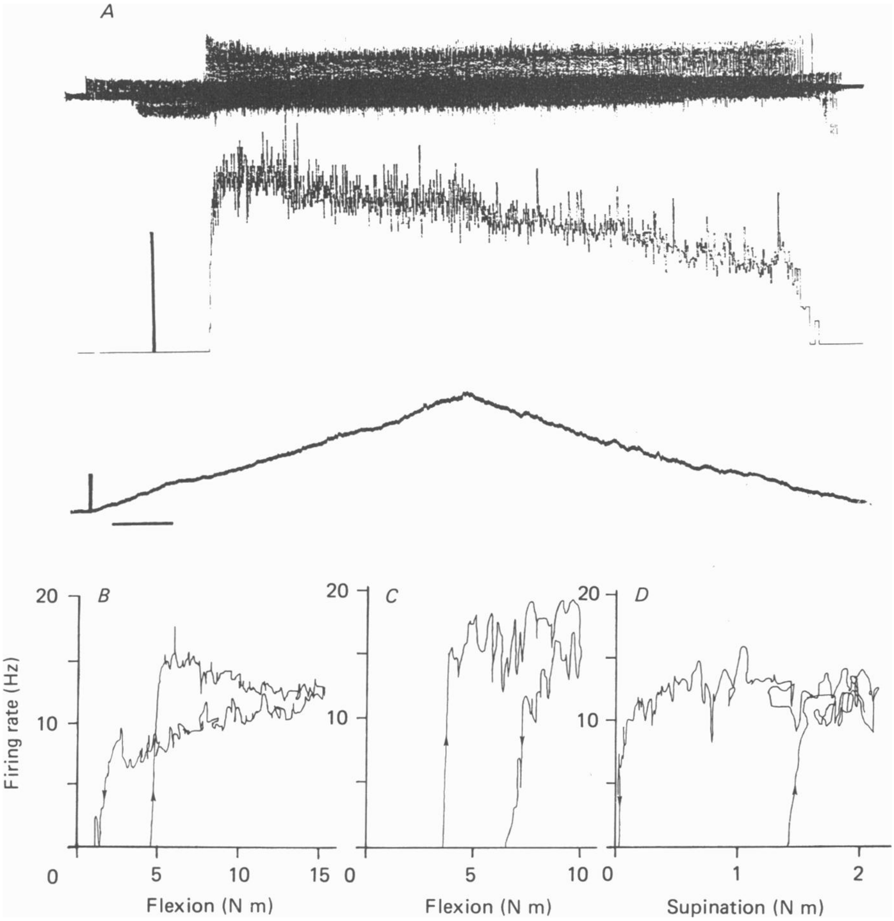

Fig. 1. *A*, intramuscular e.m.g. (upper trace), instantaneous firing rate (unfiltered, middle trace) and voluntary exerted force in flexion direction (lower trace). The motor unit was located medially in the long head of the biceps. In the e.m.g. recording another action potential which points downwards is seen which disappears as soon as the unit under study recruits. This action potential reappears when the unit under study decruits. It was confirmed that only the amplitude of this action potential changed and that this unit did not really stop firing. The change was probably caused by the contraction of the muscle changing the position of the recording electrodes in the muscle. Calibration bars: firing rate: 10 Hz; flexion force: 5 N m; time: 5 s. *B–D*, firing rate as a function of total force. Arrows indicate the sequence in which the trajectories are completed. *B*, the firing rate as a function of flexion force for the unit shown in *A*. *C*, firing pattern of a motor unit of the brachialis as a function of exerted flexion force. *D*, firing pattern of the same unit as shown in *A* and *B* but now when a supinating force is exerted.

Differences in the firing behaviour of motor units within the pool of synergists

Since in the biceps, decruitment thresholds were lower than recruitment thresholds, more motor units of the biceps must be active during relaxation from flexion than during contraction at the same force level. This is in keeping with the fact that the firing rates of units in the biceps are then lower. In addition to this and to the time-dependent effects mentioned in the Introduction, a contribution from the antagonists, or a decreasing contribution from functional synergists might also play a role. Therefore, we investigated the behaviour of motor units in a number of muscles simultaneously. During relaxation from flexion, the antagonist (i.e. the triceps) remained completely inactive. This was checked in several experiments with surface e.m.g. recordings and in one experiment by the insertion of wire electrodes with a large bare area. The recordings from these electrodes showed motor unit activity for even the smallest extending force, but during relaxation from flexing forces no activity was recorded.

The brachialis is sometimes considered to be the 'flexor par excellence' (McGregor, 1950). A typical example of the relation between flexion force and firing rate of a motor unit of that muscle is given in Fig. 1*C*. It appears that in the brachialis, most units stop firing at a higher force level than their recruitment threshold. During relaxation, firing rates of motor units also appeared to be lower than at corresponding force levels during contraction.

Furthermore, it seemed important to differentiate between motor units at different locations within the biceps muscle (cross-sectional diameter between 2·0 and 3·5 cm), because we found earlier that units in different parts of this multifunctional muscle behave differently for different tasks (ter Haar Romeny, Denier van der Gon & Gielen, 1984).

In Fig. 2*A* the results are shown for motor units located in the long head of the biceps at medial ($n = 8$), central ($n = 6$) and lateral ($n = 7$) sites and in the brachialis ($n = 9$). The two end-points of each line in this Figure represent the average recruitment and decruitment thresholds of a unit obtained in two to five experiments. The highest points represent the recruitment thresholds with the accompanying mean first regular firing rates in the contraction phase. Sometimes the first intervals were very irregular, e.g. corresponding to a doublet. These intervals were omitted in the analysis. The lower points represent the decruitment thresholds and the last regular firing rates. These first and last regular firing rates were obtained from graphs like the one shown in Fig. 1*B*.

As can be seen, the firing rate just before decruitment is always lower than just after recruitment. The most striking aspect is the difference in the recruitment and decruitment thresholds at the different locations in the biceps and the brachialis. At the medial and central sites of the long head of the biceps we can see that in all cases but one the decruitment threshold is lower than the recruitment threshold. The lateral site shows no significant difference in the two force thresholds. In the brachialis, however, the decruitment threshold usually appeared to be higher than the recruitment threshold.

As stressed earlier, the biceps takes part in the performance of the flexion,

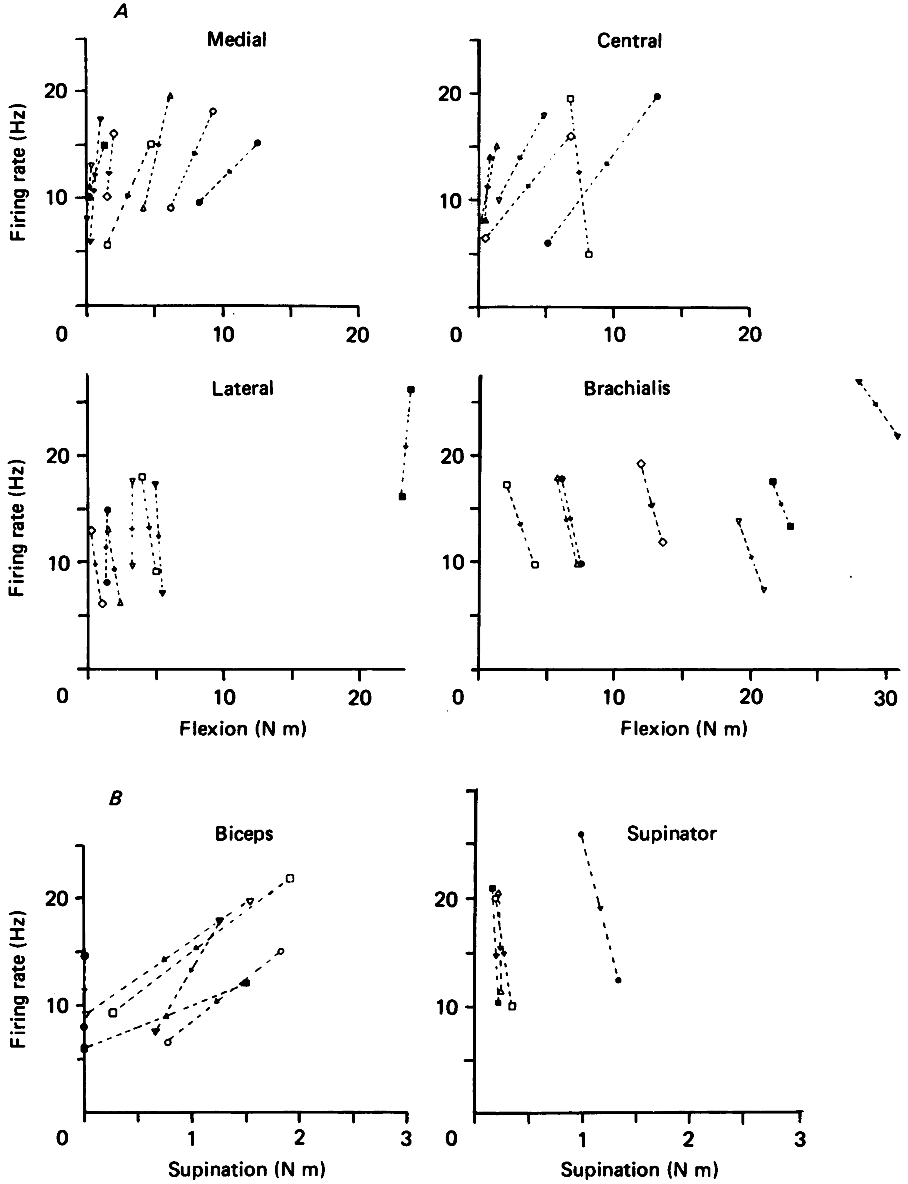

Fig. 2. Recruitment and decruitment thresholds with accompanying first and last regular firing rate. The firing rate just after recruitment is always higher than just before decruitment. *A*, motor units at medial, central and lateral locations in the long head of the biceps and in the brachialis active during flexion. *B*, motor units located medial (filled symbols) and central (open symbols) in the long head of the biceps and in the supinator active during supination.

supination and exorotation tasks. Fig. 1*D* shows the firing behaviour of the same unit as shown in Fig. 1*A* and *B*, but now the subject exerts supination force, keeping the forces in flexion and exorotation direction at zero. In the first place, we can see that the relative difference between the recruitment and decruitment threshold is much greater for supination than for flexion. In the second place, the lowering of firing rate occurs only in the very last stage of the relaxation phase. Sometimes, even higher frequencies were found when the force was lowered than at the corresponding force level during contraction. All other investigated units in the biceps (long head) which contribute to supination (located medially, $n = 3$ and centrally, $n = 3$, see ter Haar Romeny *et al.* 1984), showed similar behaviour (see Fig. 2*B*, left side). Motor units in the biceps, active during the exertion of force in exorotation direction, showed the same behaviour as during the supination task. This could be expected because there is a great similarity in the recruitment behaviour of motor units in the biceps with respect to supination and exorotation (ter Haar Romeny *et al.* 1984).

In one experiment, the phenomena were also examined in the supinator ($n = 4$, see Fig. 2*B*, right side). In this muscle the firing rate of the four recorded units was lowered during relaxation from supination. The decruitment thresholds for these units were higher than the recruitment thresholds.

In a number of experiments directed to other questions, the behaviour of a large number of motor units in the biceps and also five units in the brachialis did confirm the findings described here.

The role of time-dependent processes

We investigated whether time-dependent effects like fatigue and potentiation play an important role with respect to the phenomena described above. We did this by testing whether the change in apparent threshold depends on the length of time that the motor unit was firing.

The subject was asked to perform a slow ramp contraction in the flexion direction. As soon as a particular motor unit started firing, the subject was asked to keep the exerted force constant at this level for a certain time T (up to 120 s). Thereafter the exerted force was reduced again slowly (see Fig. 3*A*). The force level at which a unit stopped firing is plotted in Fig. 3*B* for a number of units in the biceps as a function of time T. As can be seen from this Figure the decruitment level does not change as a function of the time for which the unit was active. It appears that the threshold is lowered as soon as the unit starts firing or at least within about 0·5 s. It is not possible to tell exactly what happens during the first few discharges of a motor unit. The subject needs a finite time to react to the recruitment of a unit and to change from slow contraction to slow relaxation in a smooth way. During this time, the decruitment threshold already reaches its final level, which is detected in the experiments. The variability in the decruitment thresholds is of the same order as the variability in the recruitment threshold (Fig. 3*B*, left side). The same behaviour was observed for motor units of the long head of the biceps that contribute to supination when a supinating force was exerted.

When the contraction started slowly again, before the motor unit had stopped firing during slow relaxation, the firing rate quickly increased as it had done when the contraction was performed for the first time. We did not notice any effect of fatigue.

Changes in the recruitment threshold

It appeared that not only the decruitment threshold but also the recruitment threshold of a motor unit changes when the muscle involved is active. This was investigated in the following way. When the subject increased the flexion force a short

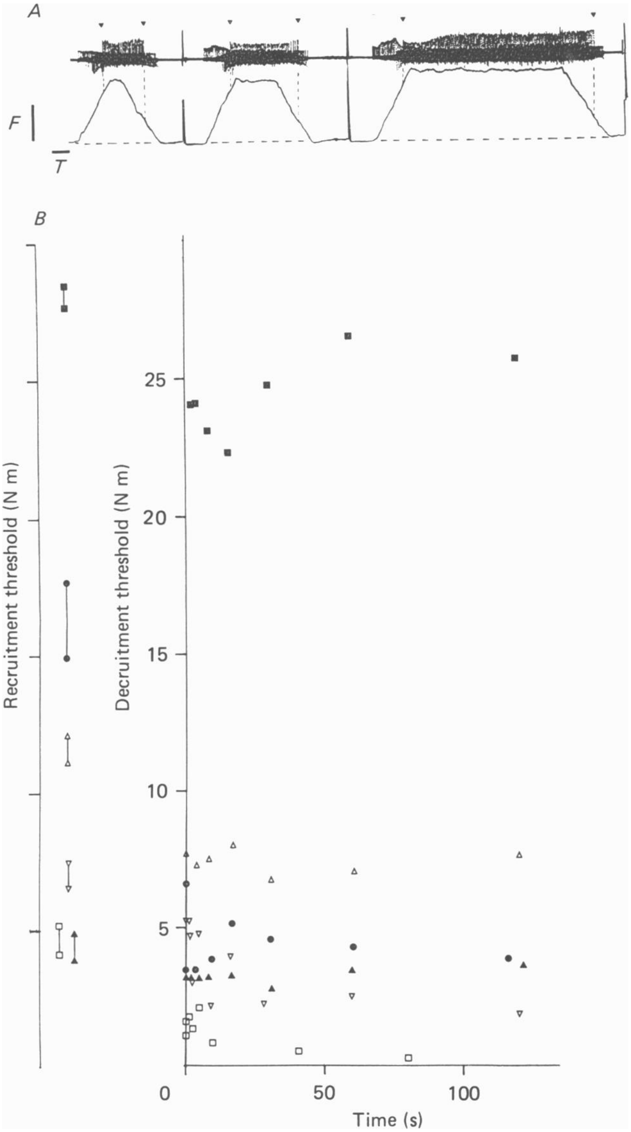

Fig. 3. *A*, the firing behaviour of the same motor unit as in Fig. 1, while force is being exerted in flexion direction, as a function of the time that elapsed after the onset of firing. Recruitment and decruitment are denoted by arrows. Time between successive recordings was at least 15 s. Vertical continuous lines denote that the recorder was stopped between successive recordings. Calibration bars: flexion force (*F*): 2 N m; time (*T*): 2 s. *B*, decruitment thresholds during relaxation from exerting force in flexion direction of several motor units of the biceps as a function of the time after the onset of firing. On the left the range of recruitment thresholds obtained is shown.

time after decruitment of a biceps unit, the recruitment threshold was found to be lower than the initial threshold. We studied the change of the recruitment threshold as a function of the time after decruitment (see Fig. 4*A*). A slow ramp contraction was performed in flexion direction until the unit under study started firing. Then,

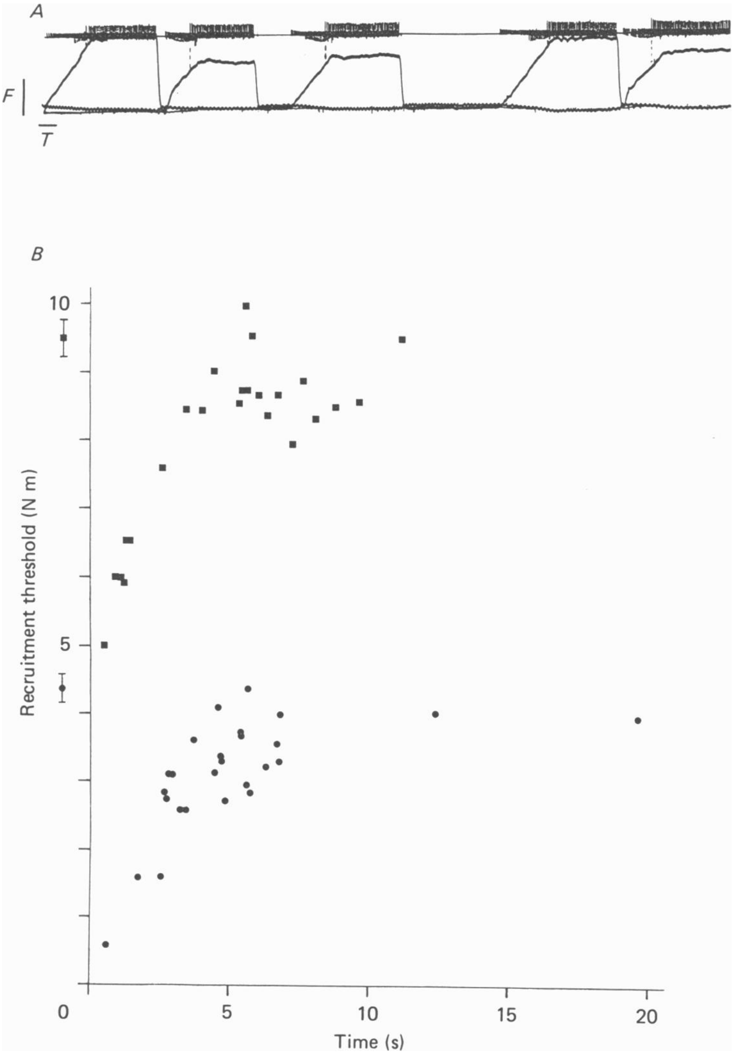

Fig. 4. *A*, firing behaviour of the same motor unit as shown in Fig. 1 while force is being exerted in flexion direction. At a variable time after complete relaxation the force is increased again and the recruitment threshold is measured. The first contraction in this Figure is also the first to be performed during the experiments and thus shows the original recruitment threshold (4·5 N m). The same remark on the disappearance of a previously active unit that was made for Fig. 1 holds for this recording. Calibration bars: force (*F*): flexion: 2 N m; supination: 0·1 N m; exorotation: 2 N m; time (*T*): 2 s. *B*, recruitment threshold for force exerted in flexion direction of two medially located motor units after complete relaxation as a function of the time between decruitment and subsequent recruitment. On the left the recruitment threshold is shown when the contraction is performed for the first time after the subject has been relaxed for a sufficiently long time. The original recruitment threshold is reached again about 4 s after complete relaxation.

after keeping the force constant for a short and constant period, the subject had to relax completely at once. After a variable time, the recruitment threshold was measured again by slowly increasing the force level according to the stimulus ramp. In Fig. 4*B*, the resultant recruitment thresholds are plotted as a function of time after decruitment of the unit. Within about 4 s after complete relaxation, the original recruitment threshold was reached again. The relatively large scatter in the data is probably due to the fact that the subject could not easily keep the other forces at zero during these abrupt relaxation experiments.

DISCUSSION

In this paper results are presented which show differences in the behaviour of motor units during slow isometric contraction and relaxation. In the first place, decruitment thresholds are often different from recruitment thresholds.

Secondly, the firing rate of the investigated units was in most cases observed to be lower during relaxation than at the same force level during contraction. These results are in agreement with findings reported by authors mentioned in the Introduction.

In Fig. 2 we have shown that the observed firing patterns of motor units differ between muscles and even parts of muscles. Both biceps (long and short head taken together) and brachialis are supposed to deliver about 30 % of the total flexion force in experimental conditions similar to ours (Jørgensen & Bankov, 1971; Cnockaert, Lensel & Pertuzon, 1975). We have also shown that motor units (e.g. the one shown in Fig. 1 *B* and *D*) behave differently depending on the task the subject has to perform.

The findings are corroborated by the experience of the subjects. They found it difficult to make a motor unit in the brachialis fire regularly without raising the force far above the recruitment threshold. Small force fluctuations make units in the brachialis stop and start firing again as long as the maintained force level is below the decruitment threshold and above the recruitment threshold. On the other hand, in the biceps it was easy to maintain a regular (low) firing rate, but often difficult to make a unit stop firing, especially during relaxation from supination or exorotation. In the biceps, only minor changes in firing rate take place even if the force level is below the recruitment threshold and provided it is above the decruitment threshold.

The above-mentioned results were evaluated by making plots of the relation between total force and firing rate of motor units. In these plots certain time delays are introduced. In the first place, the low-pass (3 Hz) analog filtering of the instantaneous firing frequency signal causes an apparent frequency delay. Secondly, the instantaneous interspike interval was determined at the end of an interval. Strictly speaking, it is more correct to attribute a detected frequency signal to the centre of the interspike interval. Finally, the *X*–*Y* recorder was too slow to record fast changing signals. In total, these delays were less than 300 ms. On the other hand, the twitch times of motor units cause an effective time lag of about 100 ms between the recording of the e.m.g. and the subsequent generation of force, which compensates to a certain extent for the above-mentioned time lag. So, in our plots there may be a time lag of about 200 ms between the detection of firing rate and the exerted force. While flexion force (contraction velocity about 1 N m/s) is being exerted this implies a maximum deviation of about 0·2 N m. This value is small compared to variations in threshold that occur in repeated experiments.

The results presented show that motor units of synergists have a very dissimilar behaviour during contraction and relaxation. An interesting question is whether this different behaviour reflects a different activation of motoneurones of synergists involved in the same task, or whether properties intrinsic to motoneurones and motor units can provide an explanation for the experimental results. It is well known that during a steadily maintained contraction, the firing rate of motoneurones declines from the time at which they were first recruited (Person & Kudina, 1972). In addition, forces generated by larger and faster units decrease, even when the firing rate remains constant. The proportion of slow and fast muscle fibres seems to be the same for arm muscles (Johnson, Polgar, Weightman & Appleton, 1973). This would imply that the average decrease in firing rate and force output of motor units will be about the same in all participating muscles. Furthermore, it appeared that the behaviour of a unit primarily depended on its location and not on its actual threshold.

Another argument against the view that differences in intrinsic properties of motoneurones and motor units may explain our findings is that if during relaxation force was increased again, the firing rate followed the same trajectory as when the contraction was performed for the first time, provided that decruitment had not yet occurred. Evidently, this argues against effects of fatigue. Moreover, it was shown that changes in the decruitment threshold were not influenced by the time that elapsed after the onset of firing.

These findings taken together lead us to the conclusion that the observed phenomena are not merely a consequence of changes in motoneuronal properties but that they reflect shifts in the activation of motoneurone populations of synergists during isometrical motor tasks.

We gratefully acknowledge the financial support of the Netherlands Organisation for the Advancement of Pure Research for this project. We wish to thank Dr D. Kernell for reading an earlier draft of this paper and giving valuable advice.

REFERENCES

Burke, R. E., Rudomin, P. & Zajac, F. E. (1976). The effect of the activation history on the tension production by individual muscle units. *Brain Research* **109**, 515–529.

Cnockaert, J. C., Lensel, G. & Pertuzon, E. (1975). Relative contribution of individual muscles to the isometric contraction of a muscular group. *Journal of Biomechanics* **8**, 191–197.

de Luca, C. J., Lefever, R. S., McCue, M. P. & Xenakis, A. P. (1982). Behaviour of human motor units in different muscles during linearly varying contractions. *Journal of Physiology* **329**, 113–128.

Desmedt, J. E. (1981). The size principle of motoneurone recruitment in ballistic or ramp voluntary contractions in man. In *Motor Unit Types, Recruitment and Plasticity in Health and Disease. Progress in Clinical Neurophysiology*, vol. 9, ed. Desmedt, J. E., pp. 97–136. Basel: Karger.

Grimby, L. & Hannerz, J. (1973). Tonic and phasic recruitment order of motor units in man under normal and pathological conditions. In *New Developments in Electromyography and Clinical Neurophysiology*, vol. 3, ed. Desmedt, J. E., pp. 225–273. Basel: Karger.

Johnson, M. A., Polgar, J., Weightman, D. & Appleton, D. (1973). Data on the distribution of fibre types in thirty-six human muscles. An autopsy study. *Journal of Neurological Sciences* **18**, 111–129.

Jørgensen, K. & Bankov S. (1971). Maximum strength of elbow flexors with pronated and supinated forearm. In *Biomechanics II, Medicine and Sport*, vol 6, ed. Desmedt, J. E., pp. 174–180. Basel: Karger.

Kukulka, C. G. & Clamann, H. P. (1981). Comparison of the recruitment and discharge properties of motor units in human brachial biceps and adductor pollicis during isometric contractions. *Brain Research* **219**, 45–55.

McGregor, A. L. (1950). *Synopsis of Surgical Anatomy*, 7th edn. Baltimore: The Williams and Wilkins Co.

Maton, B. (1981). Human motor unit activity during the onset of muscle fatigue in submaximal isometric isotonic contraction. *European Journal of Applied Physiology* **46**, 271–281.

Millner-Brown, H. S., Stein, R. B. & Yemm, R. (1973). The orderly recruitment of human motor units during voluntary contractions. *Journal of Physiology* **230**, 359–370.

O'Donovan, M. J., Pinter, M. J., Dum, R. P. & Burke, R. E. (1982). Actions of FDL and FHL muscles in intact cats: Functional dissociation between anatomical synergists. *Journal of Neurophysiology* **47**, 1126–1143.

Person, R. S. & Kudina, L. P. (1972). Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. *Electroencephalography and Clinical Neurophysiology* **32**, 471–483.

ter Haar Romeny, B. M., Denier van der Gon, J. J. & Gielen, C. C. A. M. (1982). Changes in the recruitment order of motor units in human biceps muscle. *Experimental Neurology* **78**, 360–368.

ter Haar Romeny, B. M., Denier van der Gon, J. J. & Gielen, C. C. A. M. (1984). Relation between location of a motor unit in the human biceps brachii and its critical firing level for different tasks. *Experimental Neurology* **85**, 631–650.