J. Physiol. (1978), **277**, *pp.* 143–152
With 1 *plate and* 5 *text-figures*
Printed in Great Britain

AXONAL CONDUCTION VELOCITY AND VOLUNTARY DISCHARGE PROPERTIES OF INDIVIDUAL SHORT TOE EXTENSOR MOTOR UNITS IN MAN

BY JÖRGEN BORG, LENNART GRIMBY AND JAN HANNERZ
From the Department of Neurology, Karolinska Hospital, Stockholm, Sweden

(*Received 5 October 1977*)

SUMMARY

1. The axonal conduction velocity and the voluntary discharge properties of 120 short toe extensor motor units were studied in man.

2. Electromyographic techniques were used which permitted the identification of individual motor unit potentials after proximal and distal electrical nerve stimulation and during maximum voluntary effort.

3. The necessary selectivity of the e.m.g. recordings was achieved in two circumstances. In some subjects, previous motor nerve lesions distal to the point of stimulation had led to collateral sprouting with larger motor unit potentials. In other subjects an accessory deep peroneal nerve was present, so that lidocaine block of the main motor nerve left a small number of innervated motor units.

4. The axonal conduction velocities of the individual motor units ranged from 30 to 54 m/sec with most motor units between 35 and 45 m/sec.

5. Motor units which voluntarily could be driven continuously at frequencies below 10/sec had axonal conduction velocities between 30 and 45 m/sec.

6. Motor units which on voluntary drive responded only in high frequency bursts had axonal conduction velocities between 40 and 54 m/sec.

7. Motor units with intermediate voluntary discharge properties had intermediate axonal conduction velocities.

8. Thus a relationship was established between voluntary discharge properties and axonal conduction velocity.

INTRODUCTION

It is known from animal experiments that different alpha motor axons have different conduction velocity (Erlanger & Gasser, 1937) and that the axonal conduction velocity of a motor unit is related to its contraction time (Bessou, Emonet-Dénard & Laporte, 1963; Steg, 1964), fatiguability and histochemistry (Burke, Levine, Tsairis & Zajac, 1973).

No corresponding studies have been made in man because of methodological difficulties. However, with proper electromyographic techniques individual human motor units can be identified on nerve stimulation and thus axonal conduction velocity can be studied in man.

The discharge properties of motor units on voluntary activation in man have been studied earlier and different types of motor units have been described (Grimby & Hannerz, 1977). One type of motor unit could be driven continuously and attained regular firing intervals at a rate about 10/sec. This type was called continuously discharging long interval motor unit (c.l.m.u.). Another type of motor unit could not be driven continuously and did not attain regular firing intervals at rates below 20/sec. This type was called intermittently discharging short interval motor unit (i.s.m.u.). However, large numbers of the motor units were intermediate in type.

It was suggested that c.l.m.u.s had slowly contracting, fatigue resistant type I muscle fibres and i.s.m.u.s had fast contracting, fatiguable type II muscle fibres.

The purpose of this work was to study the differences in the axonal conduction velocity of different motor units in man and determine whether the voluntary discharge properties of a motor unit are related to its axonal conduction velocity.

METHODS

The short toe extensor muscle was tested in clinically healthy subjects with normal motor conduction velocity measured with conventional techniques.

The common peroneal nerve was stimulated close to the head of the fibula. The deep peroneal nerve and the accessory deep peroneal nerve were stimulated at the ankle, anterior and posterior to the lateral malleolus respectively. The latency difference between the proximal and distal stimuli was measured.

Stimulation was by surface electrodes. The position of the cathode was adjusted so that minimum stimulus strength was required for muscle response. The anode was placed proximal to the cathode and a few centimetres from the nerve. Single shocks of 0·2 msec duration were used. The stimulus strength was just above the threshold of the motor unit under study.

All the experiments were made at the same time of the day in a room which maintained a stable temperature. The skin temperature of the lower leg was approximately the same in all the subjects, about 32 °C.

Identification of individual motor units was possible by using electromyographic recordings with high selectivity. Only motor units with potentials that could with safety be identified by their characteristic shape in voluntary contraction and in the proximal and distal electrical stimulations were studied. Bipolar needle or wire electrodes with impedances up to a few MΩ were used (Hannerz, 1974). The potentials were amplified and displayed on a Medelec oscilloscope no. 4329 and recorded on Kodak Linograph direct print paper. Special preparation of the muscle under study was necessary (see below).

RESULTS

Electromyographic recordings with sufficient selectivity to determine the voluntary discharge properties and the axonal conduction velocity of individual motor units could be obtained in two experimental situations.

1. Electromyographic studies with needle electrodes cause denervation of muscle fibres with consequent collateral sprouting and increased muscle fibre density of the motor units. Thus repeated muscle penetrations over a long period of time increase the possibility of obtaining selective electromyographic recordings. The short toe extensor muscles of the authors had previously been the object of intensive electromyographic investigations. Identification of individual motor units was much easier than in other subjects. Furthermore, the selectivity of the electromyographic recordings increased during the 6 months of the present series of experiments. A biopsy from one of the authors was taken 3 months after the last experiment (Pl. 1).

The muscle fibres were 30 % type I and 70 % type II and there was a marked type grouping forming the basis for the electromyographic selectivity.

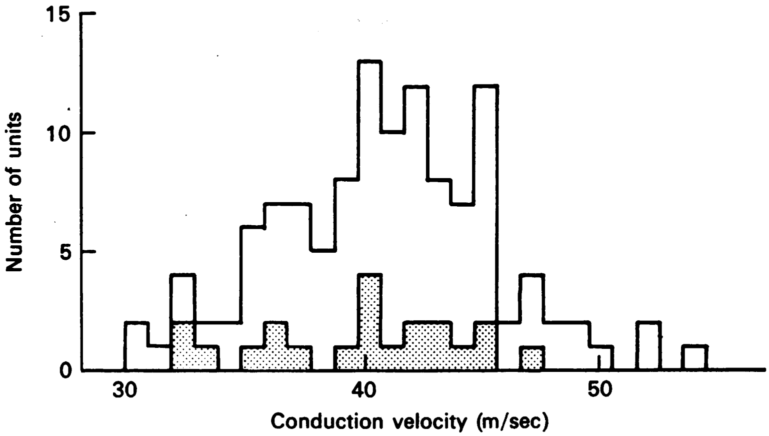
2. In about 20 % of normal subjects part of the short toe extensor muscle is innervated by an accessory deep peroneal nerve (Bryce, 1896; Lambert, 1969). In ten out of thirty young normal subjects an accessory nerve was found innervating one or a few short toe extensor motor units. The selectivity necessary for recording individual motor units was obtained by blocking the main deep peroneal nerve with lidocaine.

Text-fig. 1. Axonal conduction velocity of a single motor unit in subject L.G. *A* and *B* maximum voluntary effort. *C* proximal and *E* distal nerve stimulation just subliminal for the test unit. *D* proximal and *F* distal nerve stimulation at slightly increased intensity. Time bar in *A* 100 msec otherwise 10 msec. Further description in text.

It was comparatively easy to adjust the position of the recording electrode so that the potential of one motor unit was clearly distinguished on maximum voluntary effort. On nerve stimulation, however, the synchronization of the activity from motor units distant from the electrode made identification of the test unit potential more difficult. This was particularly the case at the distal stimulus point. Text-fig. 1 shows that the test unit can be identified on nerve stimulation in spite of considerable activity from distant motor units provided the test unit potential has a characteristic shape. In Text-fig. 1 *B* the test unit is easily identified on maximum voluntary effort by the characteristic shape and high amplitude of its potential. Text-fig. 1 *C* and *E* show the response to proximal and distal nerve stimulations, respectively, just subliminal for the test unit. Text-fig. 1 *D* and *F* show the response to slightly higher stimulus intensity with appearance of the characteristic test unit potential. The two stimulus points were 40 cm apart, the latency difference 9·5 msec, i.e. the conduction velocity of the test unit was 42 m/sec. The distal delay (6 msec) is longer than would occur in a subject who had no previous interference with the nerve terminals.

The range of axonal conduction velocities

One hundred and twenty motor units were investigated as to their axonal conduction velocity and voluntary discharge properties. Ninety-nine motor units were obtained from three subjects in whom the muscle fibres had become type-grouped, twenty-one from the ten subjects with accessory nerves to the short toe extensor muscle.



Text-fig. 2. Range of axonal conduction velocities of 120 short toe extensor motor units in thirteen subjects. Dotted squares from subjects with accessory nerve, white squares from subjects J.B., L.G. and J.H. Further description in text.

Text-fig. 2 shows that there was a continuum of axonal conduction velocities of individual motor units from 30 to 54 m/sec. The dotted part of the histogram consists of the axonal conduction velocities obtained from the subjects with accessory nerves, the undotted parts from the group of subjects with type-grouped muscles. There was no significant difference between the two groups with regard to the range of axonal conduction velocities. One of the subjects with type-grouped muscles also had an accessory nerve. Comparison between the nerve conduction velocities of ten motor units obtained by stimulating the main nerve branch and ten motor units obtained by stimulating the accessory nerve showed no difference.

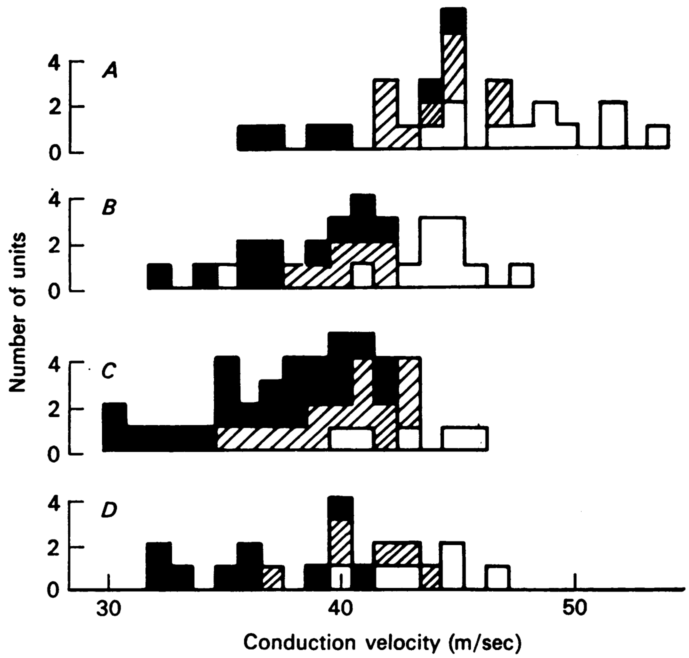
Text-fig. 2 also shows that there was no obvious bimodal distribution of axonal conduction velocities. About half of the motor units had velocities of 40 to 45 m/sec. Motor units conducting slower than 35 m/sec or faster than 50 m/sec were scarce.

The relation between voluntary discharge properties and axonal conduction velocity

As mentioned in the introduction the motor units could be differentiated into continuously discharging long interval motor units (c.l.m.u.s), intermittently discharging short interval motor units (i.s.m.u.s) and intermediates by their voluntary discharge properties.

Text-fig. 3 shows that the axonal conduction velocities were closely correlated to the voluntary discharge properties of the individual motor units in the different subjects.

The c.l.m.u.s (black on the histograms) had the lowest axonal conduction velocities ranging from 30 to 45 m/sec. The i.s.m.u.s (white) had the highest axonal conduction velocities ranging from 40 to 54 m/sec, with one exception. The axonal conduction velocity of intermediates (hatched) was on the average faster than c.l.m.u.s but slower than i.s.m.u.s but there was considerable overlapping.



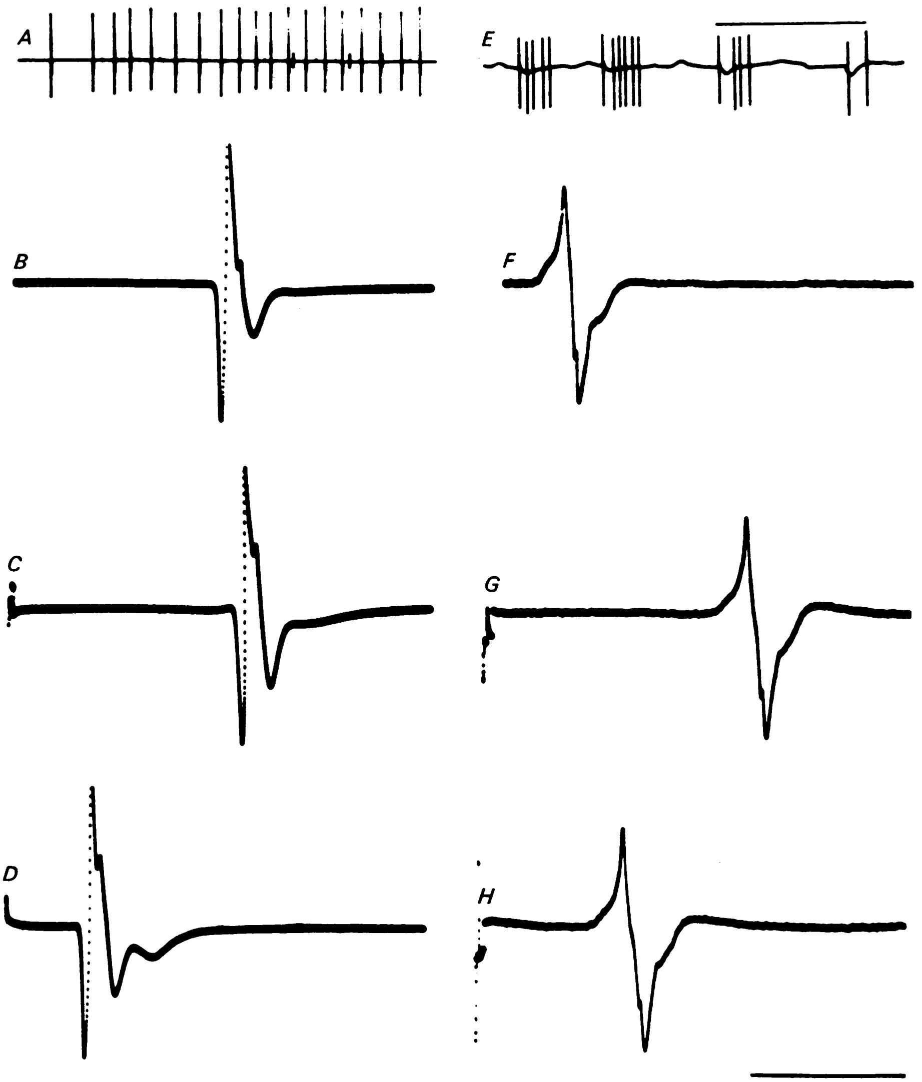
Text-fig. 3. Relation between axonal conduction velocity and voluntary discharge properties. *A* subject J.H., aged 38, *B* subject L.G., aged 43, *C* subject J.B., aged 28. *D* ten subjects with accessory nerve aged 25–30. C.l.m.u.s (filled), i.s.m.u.s (open), intermediates (hatched). Further description in text.

Text-fig. 3 also shows considerable differences between subjects. Subject A had higher minimum and maximum axonal conduction velocities for both c.l.m.u.s and i.s.m.u.s than subject C. In subject A i.s.m.u.s and intermediates predominated, while in subject C c.l.m.u.s played a greater role. The biopsy in Pl. 1 showing 70 % type II muscle fibres and 30 % type I fibres was taken from the subject with few c.l.m.u.s. The differences in axonal conduction velocities of the three authors were not related to their age.

Text-fig. 4 shows the differences between one c.l.m.u. (left) and one i.s.m.u. (right) in one of the authors using the same stimulation points.

Text-fig. 4*A* shows the c.l.m.u. firing at its minimum rate in voluntary contraction. Text-fig. 4*B* shows the shape of the c.l.m.u. potential in voluntary contraction at higher sweep speed. Text-fig. 4*C* shows the response to electrical stimulation at the head of the fibula. Text-fig. 4*D* shows the response to stimulation at the ankle. The distance between the stimulation points was 38 cm, the latency difference 10 msec, i.e. the axonal conduction velocity of the c.l.m.u. was 38 m/sec.

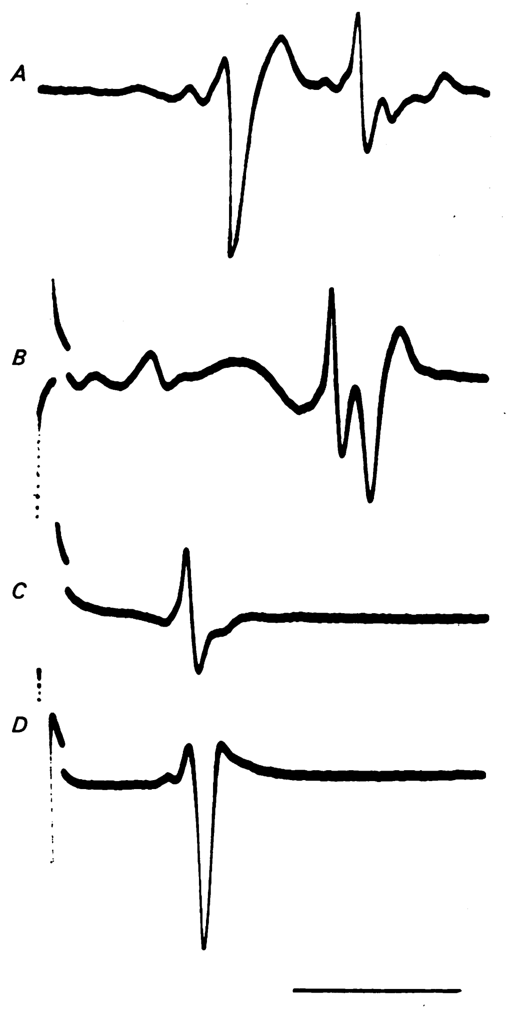
Text-fig. 4*E* shows the i.s.m.u. firing in high frequency bursts on maximum voluntary effort. Text-fig. 4*F* shows the shape of the i.s.m.u. potential on voluntary



Text-fig. 4. Axonal conduction velocity of one c.l.m.u. (left) and one i.s.m.u. (right) in subject J.H. *A* and *E* attempts to continuous voluntary discharge, *B* and *F* maximum voluntary effort, *C* and *G* proximal nerve stimulations, *D* and *H* distal nerve stimulations. Time bar in *A* and *E* 100 msec, otherwise 10 msec. Further description in text.

contraction at higher sweep speed. Text-fig. 4*G* and *H* show the response to electrical stimulation at the same sites as in 4*C* and *D* respectively. The latency difference is 7·5 msec, i.e. the axonal conduction velocity of the i.s.m.u. was 51 m/sec.

Text-fig. 5 shows the difference in axonal conduction velocity between one c.l.m.u. and one i.s.m.u. recorded simultaneously with one electrode in the author with an accessory deep peroneal nerve. Text-fig. 5*A* shows that no potentials other than those of the two motor units were recorded on maximum voluntary effort. In Text-fig. 5*B* both potentials appear on electrical stimulation of the common peroneal



Text-fig. 5. Axonal conduction velocities of one i.s.m.u. and one c.l.m.u. simultaneously recorded in subject L.G. *A* maximum voluntary effort, *B* proximal stimulation of the common peroneal nerve, *C* distal stimulation of accessory nerve branch, *D* distal stimulation of main nerve branch. Time bar 10 msec. Further description in text.

nerve at the head of the fibula. In Text-fig. 5*C* the accessory nerve was stimulated at the ankle and only the i.s.m.u. responded. The distance between the stimulus points activating the i.s.m.u. was 40 cm, the latency difference 8·7 msec, i.e. the axonal conduction velocity of the i.s.m.u. was 46 m/sec. In Text-fig. 5*D* the main branch of the peroneal nerve was stimulated at the ankle and only the c.l.m.u.

responded. The distance between the stimulation points was 40 cm and the latency difference 10·5 msec, i.e. the axonal conduction velocity of the c.l.m.u. was 38 m/sec.

DISCUSSION

No method permitting studies of the conduction velocity of individual axons in man has previously been described. Techniques for study of the latency of a motor unit potential after stimulation of its motor nerve have been available (Freund, Wita & Sprung, 1972). However, such studies provide no satisfactory information of the axonal conduction velocity since identifiable motor unit potentials are often derived from motor units with a long distal delay (cf. Text-figs. 1, 4 and 5).

Most of the experiments were made after collateral sprouting. The axonal conduction velocities obtained are representative of normal motor units only if the sprouting is due to lesions distal to the nerve stimulation points. We suggest that the sprouting of the test units was due to such distal lesions for the following reasons: At least part of the sprouting was caused by needle penetrations of the muscle with damage to the terminal nerve twigs and muscle fibres. No other aetiology was known. The motor conduction velocities obtained with conventional techniques were normal. The distal delay was, however, abnormal (cf. Text-figs. 1, 4 and 5).

Some of the experiments were made on motor units innervated by an accessory deep peroneal nerve the exact length of which, compared with the length of the main deep peroneal nerve, is not known. There was, however, no major difference in the range of axonal conduction velocity between motor units of the accessory and main branches. We suggest that the difference in length between the two branches was of minor importance.

The good agreement between the results obtained after collateral sprouting and those obtained after blockade of the main motor nerve supports the foregoing suggestions that the results are representative of axonal conduction velocities in normal man.

The methods used in this study are too complicated to be used in routine clinical work. They may, however, have a practical value since they can be used to check the reliability of more simple methods applicable to patients (Hopf, 1962).

The axonal conduction velocities of individual short toe extensor motor units in man ranged between 30 and 54 m/sec. The range of axonal conduction velocities found in this study was greater than that found with indirect techniques in man (Hopf, 1962) but was in good agreement with the range found in animal experiments (Bessou, Emonet-Dénard & Laporte, 1965; McPhedran, Wuerker & Henneman, 1965; Wuerker, McPhedran & Henneman, 1965).

Motor units which voluntarily could be driven continuously at frequencies below 10/sec had axonal conduction velocities between 30 and 45 m/sec and motor units which on voluntary drive responded mainly in high frequency bursts had axonal conduction velocities between 40 and 54 m/sec. Thus the axonal conduction velocity was found to be closely related to the voluntary discharge properties of the individual motor units.

The axonal conduction velocity of a motor unit is related to the histochemistry, the twitch time, twitch amplitude of its muscle fibres and inversely to the input resistance and after hyperpolarization of its motoneurone (Burke, 1967; Burke, Levine, Tsairis & Zajac, 1973). Since the voluntary discharge properties are related to the axonal conduction velocity, the discharge properties should also be related to the other parameters.

The voluntary discharge properties are easy to study in man whereas the other parameters are difficult or impossible to study. Thus the voluntary discharge properties may be a valuable index of the other parameters of a motor unit. We must emphasize, however, that the voluntary discharge properties of a motor unit are partly dependent on the synaptic input from muscle receptors so that they cannot be used as an index of the other parameters when this input is severely disturbed (Grimby & Hannerz, 1976).

There was a continuum for the voluntary discharge properties (Hannerz, 1974) as well as for the axonal conduction velocities with no obvious signs of bimodality. This agrees with the findings of the axonal conduction velocities of cat hindlimb (Wuerker *et al.* 1965; Burke, 1967). Neither were there any signs of bimodality in the calibre spectra of motor nerves in man (Rexed, 1944).

The muscle fibre parameters are, however, bimodal. We have therefore defined two extreme groups of motor units, the c.l.m.u. and the i.s.m.u. We conclude that motor units which discharge continuously with long intervals and have low axonal conduction velocity have slowly contracting fatigue resistant type I muscle fibres and motor units which discharge intermittently with brief intervals and have high axonal conduction velocity have fast contracting, fatiguable type II muscle fibres.

This investigation was supported by grants from the Swedish Research Council (project no. B 78-04X-04749-03).

REFERENCES

Bessou, P., Emonet-Dénard, F. & Laporte, Y. (1963). Relation entre la vitesse de conduction des fibres nerveuses motorices et le temps de contraction de leurs unités motorices. *C. r. Acad. Sci.* **256**, 5625–5627.

Bessou, P., Emonet-Dénard, F. & Laporte, Y. (1965). Motor fibres innervating extrafusal and intrafusal muscle fibres in the cat. *J. Physiol.* **180**, 649–672.

Bryce, T. H. (1896). Long muscular branch of the musculocutaneous nerve of the leg. *J. Anat.* **31**, 5.

Burke, R. E. (1967). Motor unit types of cat triceps surae muscle. *J. Physiol.* **193**, 141–160.

Burke, R. E., Levine, D. N., Tsairis, P. & Zajac, F. E. (1973). Physiological types and histochemical profiles in motor units of the cat gastrocnemius. *J. Physiol.* **234**, 723–748.

Erlanger, J. & Gasser, H. S. (1937). *Electrical Signs of Nervous Activity.* Philadelphia: University of Pennsylvania Press.

Freund, H. J., Wita, C. W. & Sprung, C. (1972). Discharge properties and functional differentiation of single motor units in man. In *Neurophysiology Studied in Man*, ed. Somjen, G. Amsterdam: Excerpta Medica.

Grimby, L. & Hannerz, J. (1977). Firing rate and recruitment order of toe extensor motor units in different modes of voluntary contraction. *J. Physiol.* **264**, 865–879.

Hannerz, J. (1974). Discharge properties of motor units in relation to recruitment order in voluntary contraction. *Acta physiol. scand.* **91**, 374–384.

Hopf H. C. (1962). Untersuchungen über die Unterschiede in der Leitgeschwindigkeit motorischer Nervenfasern beim Menschen. *Dtsch. Zsch. Nervenheilk.* **183**, 579–588.

Lambert, E. H. (1969). The accessory deep peroneal nerve. A common variation in innervation of extensor digitorum brevis. *Neurology, Minneap.* **19**, 1169–1176.

McPhedran, A. M., Wuerker, R. B. & Henneman, E. (1965). Properties of motor units in a homogeneous red muscle (soleus) of the cat. *J. Neurophysiol.* **28**, 71–84.

PADYKULA, H. A. & HERMAN, E. (1955). The specificity of the histochemical method for adenosine triphosphatase. *J. Histochem. Cytochem.* **3**, 170–183.

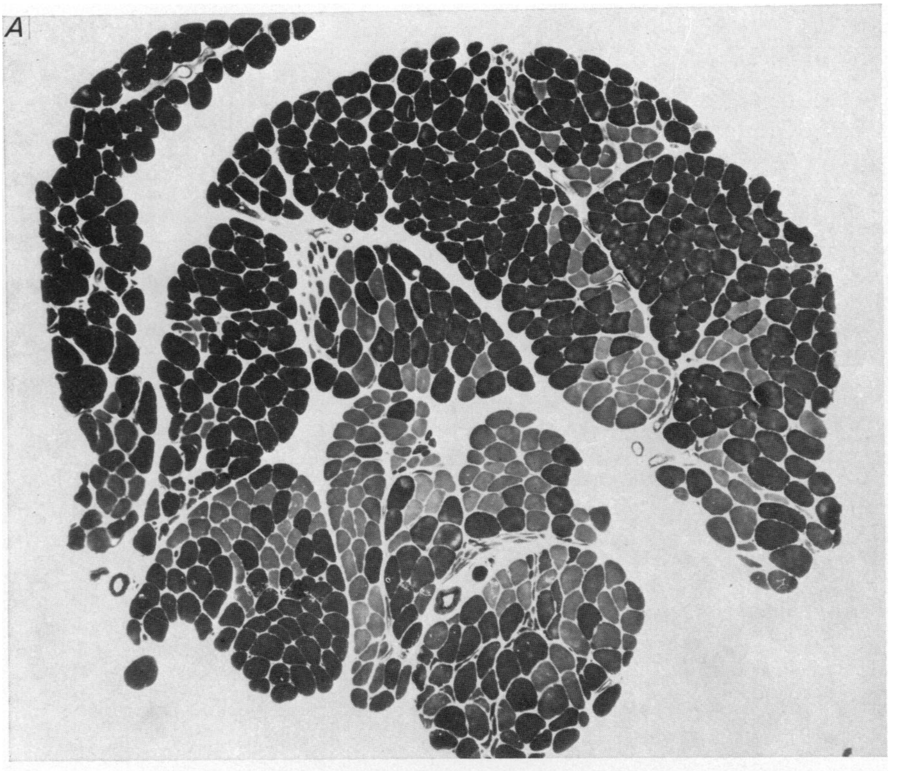
REXED, B. (1944). Contributions to the knowledge of the postnatal development of the peripheral nervous system in man. A study of the bases and scope of systematic investigations into the fibre size in peripheral nerves. *Acta psychiat. neurol. scand.* suppl. XXXIII.

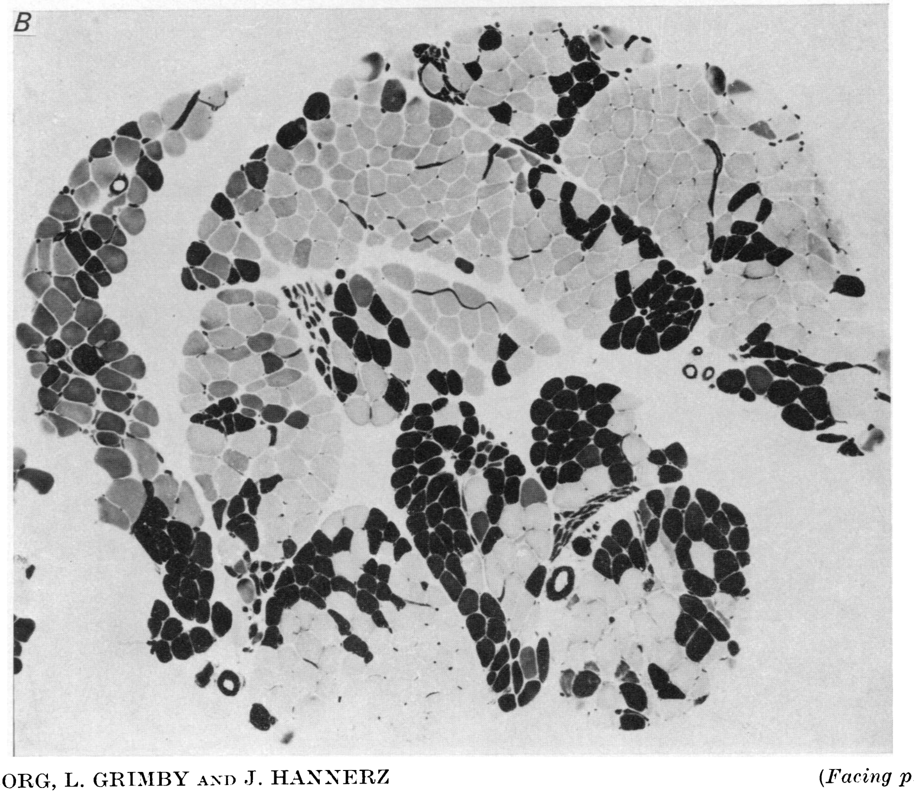
STEG, G. (1964). Efferent muscle innervation and rigidity. *Acta physiol. scand.* **61**, suppl. 225, 1–53.

WUERKER, R. B., McPHEDRAN, A. M. & HENNEMAN, E. (1965). Properties of motor units in a heterogeneous pale muscle (m. gastrocnemius) of the cat. *J. Neurophysiol.* **28**, 85–99.

EXPLANATION OF PLATE

Type grouped short toe extensor muscle in subject J.H. stained for ATP-ase, *A* pH 9,4, *B* pH 4,6, according to the method of Padykula & Herman (1955). Further description in text.





J. BORG, L. GRIMBY AND J. HANNERZ