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PROPORTION OF FATIGUE-RESISTANT MOTOR UNITS IN HINDLIMB MUSCLES OF CAT AND THEIR RELATION TO AXONAL CONDUCTION VELOCITY

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SUMMARY

1. A study of motor units to hindlimb muscles of cat has been made, with as complete a sample as possible of the motor axons to an individual muscle. In single experiments as much as 95% of the motor supply to a muscle has been examined.

2. The following muscles have been studied: peroneus brevis, peroneus tertius, peroneus longus, plantaris, gastrocnemius medialis, soleus, tenuissimus and lumbricalis superficialis.

3. Units were identified as slow resistant (S), fast resistant (FR), fast fatigable (FF) and fast intermediate (FI). The proportion of various motor unit types differs from one muscle to another. There is also some variation in the proportions to a given muscle from one animal to another. With the exceptions of soleus, which is entirely slow resistant, and gastrocnemius, which has relatively fewer resistant units, most muscles contain 60% or more of resistant (S and FR) units.

4. The conduction velocity ranges of FF, FR and FI units overlapped. There was little overlap between the conduction velocity ranges of these F units and of S units.

5. In individual experiments there was a strong and significant positive correlation between the logarithm of maximal tetanic tension and axonal conduction velocity in S, and in S+FR units. In terms of contractile response the total fatigue-resistant population appeared to be a continuum. The correlation coefficient between maximal tetanic tension and conduction velocity was also high in the totality of units of all types, although within the FF group there appeared to be little or no correlation. In pooled data there was much more scatter and these relations were less clear. This resulted largely from differences in the ranges of axonal conduction velocity for a given motor unit type from one animal to another.

6. There was a highly significant negative correlation between isometric twitch contraction time and axonal conduction velocity in individual experiments. This relationship could also be seen, but less clearly, in pooled data.

7. The possible bases for these relationships are discussed.

INTRODUCTION

Several studies have shown a relation between the amount of tension developed by a motor unit and the conduction velocity of its axon, at least for motor axons of slower conduction velocity. Thus Bessou, Emonet-Dénand & Laporte (1963) found that twitch tension showed a positive correlation and twitch contraction time a negative correlation with axonal conduction velocity in lumbricalis profondus muscle of the hind foot of cat. Wuerker, McPhedran & Henneman (1965) observed the same to be true in the motor units of medial gastrocnemius supplied by the slower axons. Olson & Swett (1966) also noted a relationship between maximal tetanic tension and conduction velocity in motor units giving relatively smaller tension responses. Appelberg & Emonet-Dénand (1967) found that tetanic tension and twitch contraction time were correlated with axonal conduction velocity over the entire range of the latter in motor units of lumbricalis superficialis of cat (see also Emonet-Dénand, Laporte & Proske, 1971). In flexor digitorum longus of cat Bagust, Knott, Lewis, Luck & Westerman (1973) also noted that log maximal tetanic tension was approximately linearly related to axonal conduction velocity while there was an inverse relationship between contraction time and conduction velocity. In peroneus tertius Jami, Murthy, Petit & Zytnicki (1982) found an approximately linear relation between log tetanic tension and axonal conduction velocity. In a comparison of four hindlimb muscles of cat (peroneus brevis, peroneus longus, soleus and tibialis anterior) and using a technique of collecting data in classes of 5 m/s conduction velocity Jami & Petit (1975) showed a nearly linear correlation between log tetanic tension and conduction velocity. This relation was similar in the four muscles although their ranges of conduction velocities differed considerably.

Following the introduction by Burke, Levine, Zajac, Tsairis & Engel (1971) of physiological tests permitting the characterization of motor units according to twitch contraction times, the presence of ‘sag’ and resistance to fatigue, investigations have been carried out on the relation between contractile responses and axonal conduction velocity of different types of motor unit in a number of hindlimb muscles of the cat. Four categories of motor units are generally recognized: slow resistant (S), fast resistant (FR), fast fatigable (FF) and fast intermediate (FI).

Although Mosher, Gerlach & Stuart (1972) found no consistent relation between conduction velocity and force or speed of contraction in motor units of soleus and tibialis anterior, most investigators have found some degree of correlation between conduction velocity and tetanic tension in S units. Proske & Waite (1974) found an apparent correlation between tetanic tension and conduction velocity in both FR and S units, but a re-examination of their data (Proske & Waite, 1976) showed that this correlation was significant only in S units.

The relationship between motor unit contractile response and axonal conduction velocity is clearer in data from individual animals than in data pooled from a number of experiments. Bagust (1974), Proske & Waite (1974) and Zajac & Faden (1985) noted that there was greater scatter in these relations in pooled data than in those from individual experiments.

An important determinant of the physiological capability of a given muscle is its composition of motor units. The several types of motor unit exist in different proportions in various muscles. While the time course of twitch contraction of a whole muscle gives some indication as to its composition of fast and slow units, it does not provide any detailed information on motor unit composition, especially the content of S units. Difficulties in sampling of the more slowly conducting motor units may lead to an underestimation of the proportion of S units. Proske & Waite (1974) drew attention to this problem in experiments in which intracellular penetration of motoneurones is used to isolate motor units. Since smaller motoneurones are associated with more slowly conducting axons, the proportion of S units might be underestimated.

The aim of the present work is to provide a more accurate determination of the motor unit composition and of the relationships between axonal conduction velocity and contractile response in the several types of motor unit of various hindlimb muscles. To that end we have studied, in each individual animal, as complete a sample of the motor unit population to a given muscle, or portion thereof, as possible by systematically examining all the ventral root filaments supplying axons to it, with care being taken to isolate axons over the full range of conduction velocities. It has been possible to study, in this manner, as much as 75–95 % of the motor supply to a muscle or a portion thereof.

It will be shown that the proportion of slow resistant motor units is higher than generally thought and that the total fatigue-resistant population (R = S + FR) comprises considerably more than the majority of the motor unit population in most of the muscles examined; that the composition of motor units in a particular muscle is distinctive, although it shows variation from one animal to another; that there is a very high correlation between axonal conduction velocity and contractile response in S and FR units; and that, from a number of physiological standpoints, S and FR units form a functional continuum.

METHODS

Experiments were carried out on adult cats of either sex, weighing between 2·2 and 4·8 kg. They were anaesthetized with an initial dose of sodium pentobarbitone intraperitoneally (45 mg/kg) supplemented with additional doses intravenously as necessary to maintain full anaesthesia. A laminectomy was performed to expose the lumbosacral cord and the skin flaps elevated to form a pool which was filled with paraffin oil. The nerve to the muscle to be studied was freed and the tendon of the muscle isolated, cut and attached to a tension transducer (Kulite load cell, range 100 or 300 g). Other nerves to the hindlimb were denervated. The region of the muscle was also formed into a pool filled with paraffin oil. It and the body of the animal were maintained at 37–38 °C by heating elements controlled by thermosensors and regulators (Yellow Springs Instruments).

The muscle length was adjusted to a level of initial tension judged sufficient to produce maximal twitch tension. Since the strain gauge was selected to have maximal sensitivity for individual motor unit responses, its range was often too small to record the total muscle twitch tension on nerve stimulation. The estimated optimal length was, in many cases, checked while stimulating a portion of the ventral root outflow that produced a twitch within the range of the transducer.

The dorsal and ventral roots were cut near their entry into the spinal cord and the cord either retracted laterally or removed. Ventral roots were split under oil into filaments and raised onto a platinum iridium electrode which was used as the anode. A similar electrode was placed on the body mass near the root entry through the dura and served as the cathode. Impulses of motor axons were detected by electrodes placed on the muscle nerve which was elevated into oil. The potentials were amplified by Grass AC amplifiers and displayed on a Nicolet or Gould digital oscilloscope. Stimulus strength was adjusted to approximately twice threshold.

Stimulation sequences and data collection were carried out using an IBM PC computer with a Tekmar Labmaster card. Following isolation of a single motor axon to the muscle under study, it was stimulated at rates of 10, 20, 30, 40 and 200/s for a duration of 0·7 s. Three twitch responses were then recorded and averaged to give measures of twitch tension and contraction time. This was followed by tetanic stimulation lasting 0·8 s with intervals between shocks of 1·25 times the contraction time, for the measurement of sag. The above stimulations were each separated by a period of 13 s. The fatigue test consisted of a series of thirteen equally spaced stimuli at an interval of 25 ms, repeated 1/s.

The criterion for determining motor unit type was similar to that described by Burke *et al.* (1971; also Burke, Levine, Tsairis & Zajac, 1973) except that the fatigue test was extended to 4 min to better differentiate the FR and FI units. At the onset of the fatigue test some units showed an initial increase in tetanic tension, others a decrease (Reinking, Stephens & Stuart, 1975; see also Kernell, Eerbeck & Verhey, 1983). The ratio of the tension obtained 2 min after the early maximum to that maximal value was measured as well as the ratio after 4 min of total stimulation. FF units were defined as those whose tension responses fell to less than 0·25 of the initial maximal value at the 2 min interval. Units with less than 0·75 but more than 0·25 of the initial maximal tension at the 2 min interval were classified as FI. Units with more than 0·75 after 2 min of stimulation but less than 0·75 after 4 min of stimulation were also considered as FI. Those with values above 0·75 after 2 and 4 min of stimulation were considered as fatigue resistant, either FR or S. FR units displayed 'sag', while S units did not.

In order to obtain as complete a sample as possible of the motor units to a given muscle in each individual experiment, we attempted to isolate and test every motor axon that was encountered. Inevitably, a certain number of units were lost because some very fine filaments containing more than one axon could not be split. The smaller the number of motor axons to a muscle and the wider their distribution in the ventral roots, the fewer were lost. In muscles small enough to study all the motor axons, the muscle nerve was left intact and it was possible to isolate from 75 to 95% of the total. When the muscle was too large to use the whole muscle nerve, a branch was selected which did not contain axons dividing into the other branches. This was often checked by stimulating the cut central ends of the other branches and observing that no contraction was produced. In this way the size of the motor pool studied could be reduced without denervating a portion of the motor units. This is a technique previously used for showing that there are no α-motor axons that are exclusively fusimotor (Ellaway, Emonet-Dénand, Joffroy & Laporte, 1972). A few experiments terminated before all the motor supply could be examined. In these between 50 and 70% of the motor unit population was examined.

When the whole muscle nerve was used, a rough estimate of the completeness of the survey of motor units could be made by relating the number of units isolated to published counts of motor axons to those muscles. Thus, gastrocnemius medialis contains about 250 motor axons, plantaris 200, peroneus tertius and brevis 70, peroneus longus 80 and tenuissimus 16 (Boyd & Davey, 1966). A further check on the fraction of the pool that was sampled came from the tally of axons lost in the isolation process. When using a branch of the muscle nerve this was the only means of judging the completeness of the survey.

In the present study we also investigated axons which innervated the lumbricalis superficialis medialis muscle (first superficial lumbrical). A number of these branched to innervate also the lumbricalis superficialis lateralis muscle (second superficial lumbrical), their motor units producing contraction in both the first and second lumbricals. In that case the tensions were added (see Appelberg & Emonet-Dénand, 1967). Motor units whose axons innervated exclusively the second lumbrical were not included.

The measure of tension responses was more satisfactory in smaller muscles which could be well separated from their neighbours. In this regard, there are particular problems in studying gastrocnemius medialis and plantaris. The circulation to gastrocnemius is such that removal of gastrocnemius lateralis may compromise the blood supply to medialis. There are also circulatory connections between the more proximal portion of plantaris and the gastrocnemii. In experiment GM1 the tendon to gastrocnemius medialis was cut and attached to the myograph, the tendons to gastrocnemius lateralis, plantaris and soleus being left intact and the ankle flexed to keep these at what was judged an appropriate length. In GM2 the tendons to these muscles were cut and tension recorded only from the tendon of gastrocnemius medialis. The most satisfactory arrangement was that used in GM3 and 4 in which we attached the myograph to the combined tendon from gastrocnemius medialis and gastrocnemius lateralis, cutting the tendons to plantaris and soleus. Because of the large mass of inactive muscle gastrocnemius lateralis in parallel with gastrocnemius medialis and the consequent need for a high initial tension for optimal tension responses, it was necessary to use a less sensitive myograph (300 g range), making it more difficult to record from units developing low tensions. A further difficulty in recording from these ankle extensors is that they are hard to free completely from surrounding connective tissue which, with the muscle exposed and skin retracted, may absorb some of the force generated. In these large and complex muscles, the location of the motor unit may also influence the amount of tension recorded. Thus, we have observed in gastrocnemius medialis that motor units producing visible contraction nearer the tendon may develop more tension than comparable units near the head of the muscle.

In gastrocnemius medialis we studied the motor units in branches containing only about $\frac{1}{4}$ of the motor supply to the muscle. If the various types of motor unit are not distributed uniformly throughout the muscle this could lead to differences in the proportions of motor unit types from one experiment to another.

The measurement of motor axon conduction velocity is subject to a certain degree of uncertainty when derived from the latency between stimulus to a ventral root filament and response recorded in the muscle nerve. While we attempted to use a stimulus strength about 2 times threshold, the actual utilization time was not known and may have varied from one unit to another. Recording from an electrode pair on the intact muscle nerve raised into oil, we used the onset of negativity at the most proximal electrode to measure the arrival of the impulse at that point. The digital oscilloscope stored a trace and measured the latency between onset of stimulus and impulse arrival. Due to afferent activity in the muscle nerve, only certain traces were satisfactory. These were selected or, in some cases, averaging was used. A small variation in latency could be seen in successive records and an increase in latency occurred during repetitive stimulation. Another, more important, source of variability was a change in conduction velocity over time. The experiments lasted up to 28 h, over which time the latency between stimulus and response in the same axon recorded near the beginning and end of the experiment sometimes changed by 0·1–0·15 ms.

The entire conducting pathway was excised from the animal at the end of the experiment, stretched taut and measured. Conduction velocity was then calculated by dividing the conduction distance by the latency between stimulus onset and beginning of impulse negativity. Subtracting a fixed value for utilization time (0·1 ms), as has been done in conduction velocity measurements in afferent axons to muscle (Hunt, 1954), produced no evident change in the relationships between tension responses and axonal conduction velocity and was therefore not routinely done.

RESULTS

The proportion of different types of motor unit in the cumulative data from the various muscles studied is shown in Table 1. It is clear that all the muscles examined contained a large fraction of S units. Except in soleus, where essentially all of the motor units are slow resistant (Burke, Levine, Salcman & Tsairis, 1974), the percentage of S units varied between 23 and 61, being generally higher among the extensor than the flexor muscles examined. The proportion of FR units also varied considerably. The percentage of all resistant units (S+FR) or R units was more consistent from one muscle to another, ranging (with the exception of soleus and lumbricalis superficialis) between 46 and 68. Apart from soleus which generally has none and lumbricalis superficialis which has very few, the fraction of FF units was more consistent: about $\frac{1}{4}$ of the total except for gastrocnemius medialis which had about $\frac{1}{3}$.

The composition of the motor unit population in the individual experiments is shown in Table 2. Here it can be seen that there was considerable variation in the proportion of the different motor unit types in a particular muscle from one animal to another. However, the percentage of R units (S+FR) was fairly consistent in a given muscle although the proportion of S units within this group showed greater variation.

The motor unit composition of peroneus brevis will be presented in detail, since it has not previously been studied. A comparison will then be made between it and the other muscles studied.

Peroneus brevis

The most extensive series (335 motor units in seven experiments) was carried out on this muscle. It is considered to be a flexor muscle, but in some circumstances behaves as an extensor (Abraham, Marks & Loeb, 1985). In three of the experiments (Table 2) the entire nerve to the muscle was left intact (series A), while in another three (series B) the branch innervating only the proximal part of the muscle was used (see Methods). It was estimated that 75–95% of the motor axons were isolated in these experiments. In an additional experiment (C), using the entire nerve, the experiment ended prematurely after about 50% of the motor axons had been studied.

TABLE 1. Proportion of various motor unit types from pooled data on eight hindlimb muscles of cat

			S		FR		FF		FI			
Muscle	Expt *n*	Axons *n*	*n*	%	*n*	%	*n*	%	*n*	%	R/all %	S/R %
P. brevis	7	335	148	44	81	24	78	23	28	8	68	65
P. longus	3	201	66	33	51	25	50	25	34	17	58	56
P. tertius	3	79	18	23	33	42	16	20	12	15	65	35
Plantaris	3	302	156	52	38	13	67	22	41	14	64	80
Soleus	1	88	88	100								
Gastroc. med.	4	223	68	30	35	16	78	35	42	19	46	66
Lumbr. sup.	4	89	57	64	15	17	5	6	12	13	81	79
Tenuissimus	3	48	13	27	13	27	10	21	12	25	54	50
Total	28	1365	614	45	266	19	304	22	181	13	64	70

R refers to S+FR units. The numbers were rounded off and the sums therefore do not always equal 100%. For abbreviations in column headings see text.

The distribution of motor unit types may be seen in Table 2. There was considerable variation in the proportion of S, FR, FF and FI units between individual animals. Thus, cat PB7 had the smallest proportion of S units (28%) and cat PB2 the largest (61%) while the average S content in all seven muscles was 44%. Since about 90% of the motor axons were examined in six of the experiments, the differences cannot be attributed to sampling error. In the animal with the highest proportion of S units both the FR and FF units occurred less frequently than on average, while in the animal with the lowest fraction of S units both FF and FR units occurred more frequently than on average. Concerning the distribution of FF and FR units, it should be noted that the FI units varied in their resistance to fatigue, some being more similar to FR units and some to FF units. Since this gradation seemed continuous, it was difficult to classify them further. On the whole, peroneus brevis must be regarded as a muscle with a large proportion of S units. The proportion of

TABLE 2. Proportion of various motor unit types from individual experiments

Muscle	Expt	No.	Sex	Wt (kg)	Side	Axons (all)	S		FR		FF		FI		R/all %	S/R %
							n	%	n	%	n	%	n	%		
P. brevis	A	5	F	4·1	R	64	35	55	15	23	12	19	2	3	78	70
	A	7	F	3·1	R	67	19	28	20	30	23	34	5	7	58	49
	A	4	M	3·1	R	60	22	37	18	30	11	18	9	15	67	55
	B	1	F	2·6	R	31	15	48	5	16	10	32	1	3	65	75
	B	2	M	2·5	R	33	20	61	5	15	6	18	2	6	76	80
	B	3	M	3·7	R	49	22	45	11	22	10	20	6	12	67	67
	C	6	M	3·1	R	31	15	48	7	23	6	19	3	10	71	68
P. longus	A	2	F	2·9	R	70	23	33	19	27	18	26	10	14	60	55
	A	1	M	2·6	R	53	20	38	12	23	15	28	6	11	60	63
	A	3	F	2·9	L	78	23	29	20	26	17	22	18	23	55	53
P. tertius	A	1	F	2·6	R	31	9	29	11	35	6	19	5	16	65	45
	A	2	M	3·0	R	21	5	24	10	48	2	10	4	19	71	33
	A	3	M	2·4	R	27	4	15	12	44	8	30	3	11	59	25
Plantaris	B	2	M	3·0	R	76	35	46	9	12	19	25	13	17	58	80
	C	1	F	2·5	R	100	51	51	5	5	28	28	16	16	56	91
	C	3	M	3·6	R	126	70	56	24	19	20	16	12	10	75	74
Gastroc. med.	B	2	F	2·3	R	69	24	35	13	19	17	25	15	22	54	65
	B	1	M	4·8	R	59	17	29	9	15	26	44	7	12	44	65
	B	4	F	3·0	L	38	13	34	6	16	16	42	3	8	50	68
	B	3	M	4·0	L	57	14	25	7	12	19	33	17	30	37	67
Lumb. sup.	A	3	F	2·8	R	34	19	56	8	24	2	6	5	15	79	70
	A	4	F	1·8	R	21	12	57	3	14	3	14	3	14	71	80
	A	5	M	2·4	R	19	15	79	—	—	—	—	4	21	79	100
	B	1	F	2·6	R	15	11	73	4	27	—	—	0	0	100	73
Tenuissimus	A	1	F	2·5	R	21	6	29	5	24	4	19	6	29	52	55
	A	2	F	2·2	R	15	3	20	3	20	5	33	4	27	40	50
	A	3	F	2·5	R	12	4	33	5	42	1	8	2	17	75	44

R refers to S+FR units. n represents the number of each type of motor unit out of all axons in an experiment. The numbers were rounded off and the sums therefore do not always equal 100%.

Table 3. Conduction velocities of various types of motor unit in seven experiments on peroneus brevis

		S			FR			FF			FI		
	Expt	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
A	4	83·8	69·0	93·9	96·8	92·2	99·7	93·5	82·4	98·2	95·0	87·2	97·9
	5	85·9	66·4	96·5	100·4	90·1	104·7	98·5	89·2	107·6	103·8	103·7	104·0
	7	88·7	74·0	99·1	104·8	98·4	109·9	105·2	98·6	108·9	107·7	104·8	109·4
B	1	74·2	62·3	82·6	87·7	80·9	90·5	86·4	82·6	88·4	90·5	90·5	90·5
	2	79·7	58·6	93·2	92·4	89·1	95·3	91·9	87·2	95·3	88·2	87·2	89·1
	3	75·4	55·8	87·4	86·2	82·0	88·4	85·7	82·0	91·4	87·3	85·5	90·3
C	6	70·8	61·6	78·9	81·9	78·4	84·8	84·5	82·1	86·2	85·3	81·6	87·5
All	1–7	80·8	55·8	99·1	95·9	78·4	109·9	95·0	82·0	108·9	94·6	81·6	109·4

FR units was, on average, 24%, ranging from 15 to 30% in individual experiments. The number of R units (S+FR) ranged from 58 to 78%.

Distribution of axonal conduction velocities. Table 3 shows that the mean conduction velocities of S axons in the seven experiments varied from 70·8 to 88·7 m/s; the overall mean was 80·8 m/s. The mean velocities of FR units ranged from 81·9 to 104·8 m/s with an overall average of 95·9 m/s, while the FF units had means from 84·5 to 105·2 m/s and an overall mean of 95 m/s. Thus, there was a considerable difference in the mean conduction velocities of the same type of motor unit axons from one animal to another.

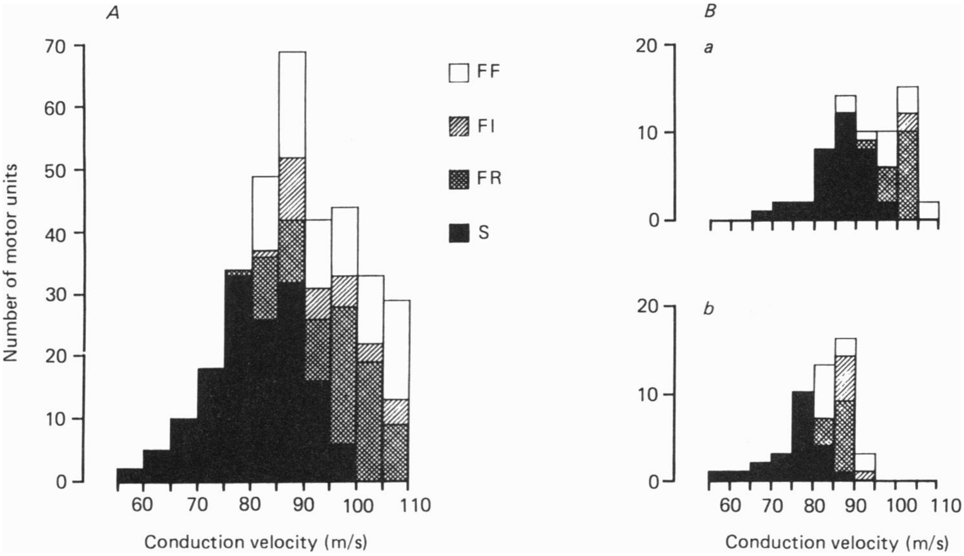

Fig. 1. Histograms of axonal conduction velocities of different types of motor unit in peroneus brevis. *A*, pooled data from seven experiments. *B*, data from two individual animals (*a* and *b*). Note the greater spread of conduction velocities of each motor unit type in the pooled data.

Figure 1 shows a histogram of the distribution of axonal conduction velocities of the several motor unit types from the pooled data of all seven experiments on peroneus brevis (*A*), as well as similar histograms from two of the individual animals (*Ba* and *b*). In the pooled data the S axonal conduction velocities ranged from 55 to 100 m/s (55·8–99·1 m/s), while the FR, FF and FI units ranged from 75 to 110 m/s (78·4–109·9 m/s). Thus, there is considerable overlap in the conduction velocities of S and the various F units; this is largely a consequence of collecting data from individual animals whose conduction velocities occupy different ranges. In individual animals some overlap was seen in the conduction velocities of S and F units. However, this overlap may not be statistically significant since within one standard deviation of the mean there was little or no overlap (see Fig. 5). It should be emphasized that the range of conduction velocities of the same type of motor unit may differ considerably from one animal to another.

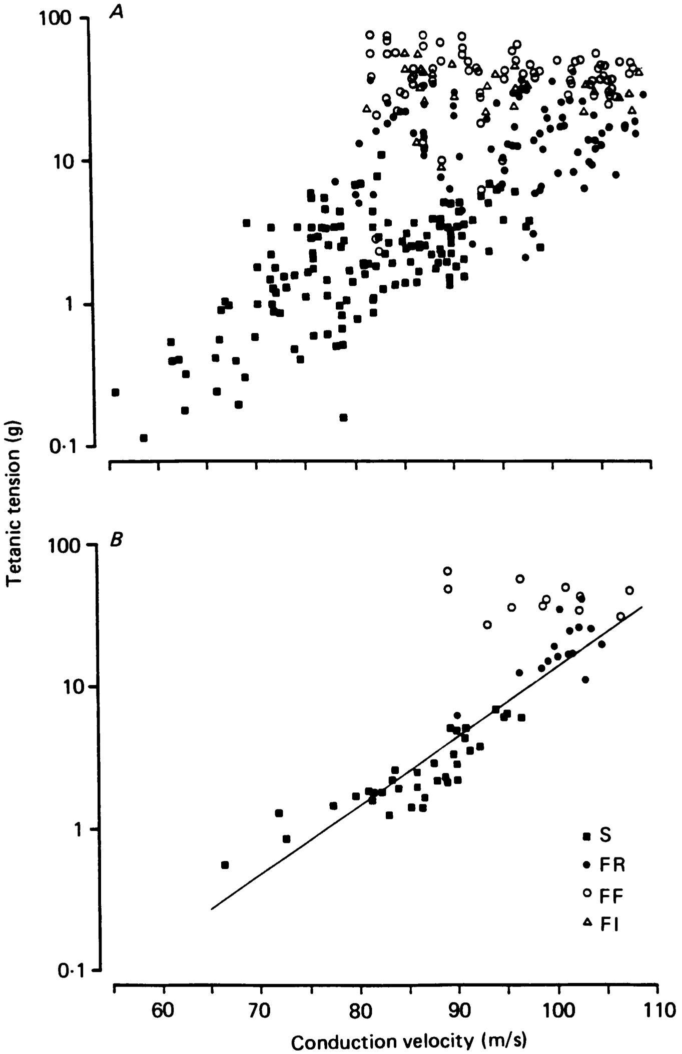

Fig. 2. Scatter plot of the relationship between maximal tetanic tension (200/s) and axonal conduction velocity in the several types of motor unit in peroneus brevis. *A*, pooled data from seven experiments. *B*, data from one animal (PB5) with linear regression line (FI units not shown). Note the much greater scatter in the pooled data. In the individual experiment the coefficient of correlation for S+FR units is 0·93 ($P < 0·001$). There was no significant correlation between tension and conduction velocity in the FF units.

Relations between axonal conduction velocity and motor unit contractile responses. Isometric tension was recorded in response to single or repetitive stimuli at frequencies between 10 and 200/s (see Methods). The tetanic tension at 200/s was considered maximal. Although this frequency is well above the physiological range, it provides a measure of the greatest contractile capacity of the motor unit.

Figure 2 is a scatter plot of the pooled data, showing the relation between log maximal tetanic tension of the several types of motor unit and axonal conduction velocity (CV) (*A*), together with a similar plot from one of the individual experiments (*B*). In the pooled data a relationship can be seen but there is considerable scatter, while in the individual experiment there is a striking, nearly linear relation between log maximal tetanic tension and conduction velocity. The pooled data for peroneus brevis has a linear correlation coefficient of 0·680 for units of all types between log maximal tetanic tension and conduction velocity, whereas in the individual experiments this value is considerably higher (see Table 4).

Table 4 compares the relationship between log maximal tetanic tension and axonal conduction velocities for S, FR, R, FF and all units in the individual experiments on peroneus brevis, as well as for the other muscles examined.

The linear coefficient of correlation between log maximal tetanic tension (at 200/s) and axonal conduction velocity in S units of peroneus brevis in individual animals ranges from 0·864 to 0·958 and is clearly significant ($P < 0{\cdot}001$). This coefficient falls to 0·649 in the pooled data on S units (Table 4). The slope of this relation (log maximal tetanic tension f(CV)) ranges from one animal to another between 0·034 and 0·061 but the main difference between individuals appears to be in the intercept of that relation with the conduction velocity axis.

When the relation between log maximal tetanic tension and conduction velocity of all fatigue resistant (S + FR) units is examined, a clear positive correlation is seen (Fig. 2*B*), without evident discontinuity between S and FR units; the linear regression line fitted to the data for S + FR units has a correlation coefficient of 0·93 ($P < 0{\cdot}001$).

As is evident from inspection of Fig. 2, there was little or no correlation between maximal tetanic tension and conduction velocity in FF units. This was confirmed by statistical analysis of the data (see below).

In four of the seven experiments on peroneus brevis there is a positive correlation between log maximal tetanic tension and conduction velocity for FR units alone with a correlation coefficient ranging from 0·694 to 0·786 and a P value of 0·05 or less (Table 4). The correlation coefficient for all R units (S + FR) was, in all cases, above 0·85 with $P < 0{\cdot}001$. It seems likely that there is a close relation between motor unit tension and conduction velocity in the FR population but that this is partially obscured by the uncertainty of conduction velocity measurement within the narrow range of conduction velocity occupied by the FR axons. As noted in Methods there are several factors that may make this measurement inaccurate and an uncertainty in the order of 0·1 ms has an important effect on the values of conduction velocity in the 90–100 m/s range. With a conduction distance of 170 mm for example, a change in latency of 0·1 ms would shift the calculated conduction velocity of 100 m/s by 5 m/s.

On inspection of the plots of the relation between log maximal tetanic tension and conduction velocity of S + FR units in individual experiments in which there was the least scatter, as in Fig. 2*B*, the points in the lower and in the upper conduction velocity ranges tended to lie above the linear regression line. A slightly better fit is provided by a curvilinear relation. To take one example, a relationship log tetanic tension $= A + B + \mathrm{CV}^2$ increased the correlation coefficients of the relation between log tetanic tension in S + FR units of the individual peroneus brevis experiments, on average, by 0·062.

FF units, in contrast to FR units, usually showed no significant correlation

TABLE 4. Correlation coefficients (Corr.) for the linear relation between log maximal tetanic tension and axonal conduction velocity for various types of motor unit in individual experiments, together with their *P* values

		S		FR		R		FF		All	
Muscle	Expt	Corr.	*P*	Corr.	*P*	Corr.	*P*	Corr.	*P*	Corr.	*P*
P. brevis	1	0·958	< 0·001	*	—	0·971	< 0·001	0·725	0·02	0·938	< 0·001
	2	0·903	< 0·001	*	—	0·922	< 0·001	*	—	0·875	< 0·001
	3	0·864	< 0·001	−0·237	0·05	0·899	< 0·001	0·131	0·8	0·869	< 0·001
	4	0·918	< 0·001	0·135	0·6	0·854	< 0·001	0·821	0·01	0·783	< 0·001
	5	0·880	< 0·001	0·694	0·01	0·930	< 0·001	−0·296	0·4	0·849	< 0·001
	6	0·909	< 0·001	0·786	0·05	0·938	< 0·001	*	—	0·938	< 0·001
	7	0·907	< 0·001	0·756	< 0·001	0·951	< 0·001	−0·042	0·9	0·889	< 0·001
	Total	0·649	< 0·001	0·048	0·7	0·732	< 0·001	0·130	0·3	0·680	< 0·001
P. longus	1	0·776	< 0·001	0·433	0·2	0·816	< 0·001	−0·025	1·0	0·713	< 0·001
	2	0·745	< 0·001	0·558	0·01	0·861	< 0·001	−0·182	0·5	0·724	< 0·001
	3	0·880	< 0·001	0·774	< 0·001	0·911	< 0·001	−0·042	0·9	0·844	< 0·001
	Total	0·013	1·0	−0·414	0·01	0·243	0·01	−0·217	0·2	0·351	< 0·001
P. tertius	1	0·630	0·07	−0·219	0·6	0·826	< 0·001	−0·338	0·6	0·744	< 0·001
	2	*	—	0·056	0·9	0·777	< 0·001	*	—	0·777	< 0·001
	3	*	—	0·960	< 0·001	0·909	< 0·001	−0·177	0·7	0·885	< 0·001
	Total	0·803	< 0·001	0·701	< 0·001	0·850	< 0·001	0·146	0·6	0·761	< 0·001
Plantaris	1	0·575	< 0·001	*	—	0·622	< 0·001	−0·378	0·5	0·720	< 0·001
	2	0·710	< 0·001	0·330	0·4	0·857	< 0·001	0·292	0·3	0·904	< 0·001
	3	0·755	< 0·001	0·465	0·03	0·815	< 0·001	−0·156	0·6	0·831	< 0·001
	Total	0·660	< 0·001	0·597	< 0·001	0·779	< 0·001	0·326	0·01	0·614	< 0·001
Soleus	1	0·873	< 0·001	—	—	—	—	—	—	—	—
Gastroc. med.	1	0·572	0·02	0·547	0·2	0·080	0·7	0·638	< 0·001	0·717	< 0·001
	2	0·858	0·01	*	—	0·921	< 0·001	0·197	0·6	0·868	< 0·001
	3	0·792	0·01	*	—	0·917	< 0·001	0·510	0·05	0·879	< 0·001
	4	0·644	0·02	0·867	0·02	0·900	< 0·001	0·022	1·0	0·793	< 0·001
	Total	0·097	0·5	−0·175	0·4	0·533	< 0·001	−0·248	0·04	0·574	< 0·001
Lumbr. sup.	1	0·689	0·02	*	—	0·894	< 0·001	*	—	0·894	< 0·001
	3	0·814	< 0·001	0·938	< 0·001	0·942	< 0·001	*	—	0·954	< 0·001
	4	0·870	< 0·001	*	—	0·924	< 0·001	*	—	0·958	< 0·001
	5	0·887	< 0·001	*	—	0·877	< 0·001	*	—	0·924	< 0·001
	Total	0·861	< 0·001	0·785	< 0·001	0·917	< 0·001	*	—	0·934	< 0·001

* A coefficient of correlation has not been included when $n < 6$.

between log maximal tetanic tension and conduction velocity (Table 4); the correlation coefficient is low, positive or negative, and was not significant except in peroneus brevis experiments 1 and 4.

The physiological discharge frequency of motor units is generally considerably less than the 200/s stimulation used to determine maximal tetanic tension (see Burke, 1981 for references). In soleus, for example, Bak, Burke & Hodgson (1984) found interspike intervals of 62 and 155 ms in two units of conscious standing cats and intervals of 33 to 67 ms during walking. Thus, it was of interest to examine the tension responses to stimulation frequencies closer to the physiological range. A representative experiment (Fig. 3) on peroneus brevis shows the relation between tetanic tension and conduction velocity at stimulation frequencies of 10, 20, 30 and 40/s. In the S units with slowly conducting axons there was relatively little increase in tension when frequency of stimulation was increased from 10 to 40/s, while for the most rapidly conducting FR units there was a considerable increase.

In the range of conduction velocities where a transition occurred from S to FR units there was no distinct separation between the two motor unit types with regard to this behaviour. This suggests that, functionally, S and FR motor units may behave as a continuum. At physiological frequencies, recruitment of S and FR units of increasing conduction velocity will add small, then progressively larger, increments of tension, but only when FF (and FI) units are recruited will very large tension increments be produced.

Contraction time. In the present study the contraction time (from onset to peak tension of the isometric twitch) was measured from an average of three twitch responses recorded at the end of a series of responses to tetanic stimulation between 10 and 200/s (see Methods). The twitch responses were therefore conditioned by this uniform series of tetanic stimuli. The amplitudes of twitch tension in the very slowly conducting S units were sometimes too small to provide reliable measures of contraction time and, hence, were not included in the data.

The relation between contraction time and conduction velocity for the pooled data on all units of peroneus brevis, together with the data from one representative animal (PB5) are shown in Fig. 4. In the individual experiment there is a highly significant negative correlation between contraction time and axonal conduction velocity in S units (coefficient of correlation = -0.866, $P < 0.001$), as well as in S+FR units (correlation coefficient = -0.916, $P < 0.001$), whereas this correlation does not appear to be significant for FF units in pooled data as well as in individual experiments. The factors that may be responsible for this correlation in fatigue-resistant units are considered in the Discussion.

Comparison of motor units in the various muscles

Apart from soleus and the lumbricalis superficialis, which have exceptionally high proportions of fatigue-resistant units (about 100 and 81% respectively), and gastrocnemius which has a low proportion (46%), the other muscles had mean values of 54–68% of R units (S+FR) (see Tables 1 and 2). Within the fatigue-resistant category, the fraction of S in the total resistant population varied considerably, mean values being as low as 35% in peroneus tertius to as high as 80% in plantaris. In some muscles there were also appreciable differences in this ratio from one animal

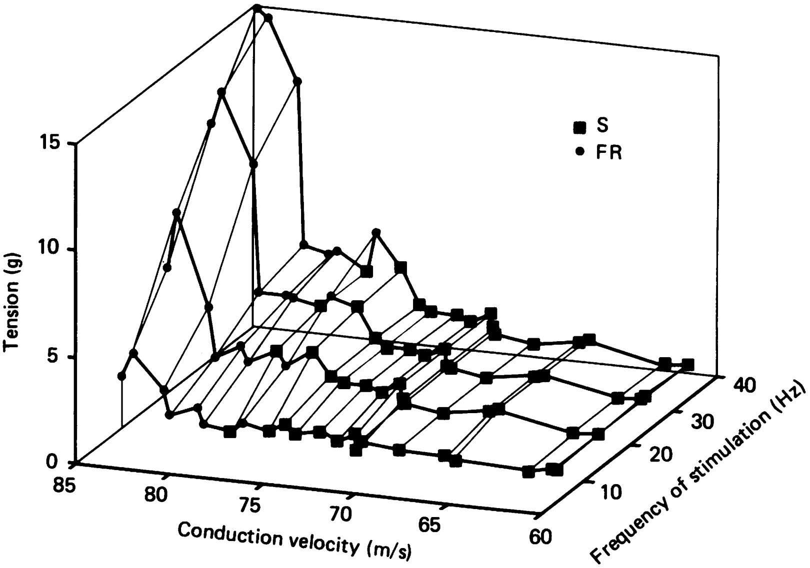

Fig. 3. Tension developed by S and FR units of an individual peroneus brevis, at varying frequencies of stimulation, as a function of conduction velocity.

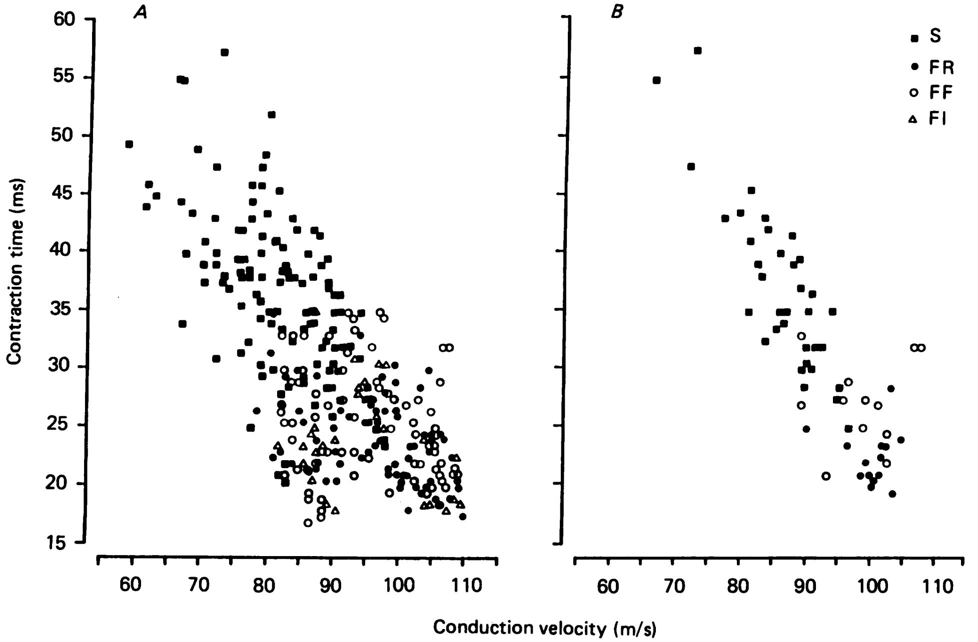

Fig. 4. Relation between isometric twitch contraction time and axonal conduction velocity in different types of motor units of peroneus brevis. *A*, pooled data from seven experiments. *B*, data from one experiment (FI units not shown). Note the greater scatter in the pooled data and the negative correlation between contraction time and conduction velocity in S and FR units.

to another. For example, in peroneus tertius the ratio S/R varied from 25 to 45% and in peroneus brevis from 49 to 80%. In other muscles the ratio was more consistent. Apart from soleus, gastrocnemius medialis and lumbricalis superficialis, the proportion of FF units was more consistent, averaging about 23%. Most of the muscles examined had nearly $\frac{2}{3}$ fatigue-resistant units. This is exclusive of FI units, some of which had an appreciable resistance to fatigue. Most muscles therefore have a majority of R units.

Kernell *et al.* (1983) compared several methods of categorizing motor units in their study of cat peroneus longus: the fatigue index of Burke *et al.* (1971), which compares the tension response to the 1st and 120th tetanus of the test; the decline in peak force in the 2 min following any initial facilitation (Kernell, Ducati & Sjöholm, 1975); or the accumulated force developed by the repeated bursts of stimulation for consecutive minutes (Reinking *et al.* 1975). All gave similar results. Kernell *et al.* (1983) also used two alternative methods of classification, one which considered all units which showed no 'sag' as slow and the other which classified as slow all units which had twitch contraction times slower than the longest contraction time of fatigable units. The latter two methods abolished the FI category and the total force attributable to S units is consequently increased. Using the second method of motor unit classification of Kernell *et al.* (1983) in which S and FR units have fatigue indices greater than 0·5 and FF units less than 0·5, while FR as well as FF units show sag but S units do not, our data show the following proportions of unit types in peroneous longus: S, 33%, FR, 42% and FF, 25%. This compares with their percentages of 21·3, 36·3 and 42·5 respectively. The values for the fraction of total tension developed by several types of motor unit in their data are S, 4·9%, FR, 31·8% and FF, 63·3%. The respective values from our data are very similar, namely 5%, 32% and 63%.

On average, the three composite extensor muscles, plantaris, gastrocnemius medialis and peroneus brevis, had roughly the same proportion of R units as did the three flexor muscles examined, peroneus longus, peroneus tertius and tenuissimus. In the extensors examined, the fraction of S units in the R population appeared to be, on average, greater than in the three flexor muscles examined (see Discussion).

A plot of the range, mean and standard deviation of the axonal conduction velocities of the several motor unit types is shown in Fig. 5 from a representative experiment for each muscle. Except for lumbricalis superficialis and peroneus tertius there is nearly total overlap in conduction velocities of all types of F units. Within one standard deviation from the mean there is very little overlap between the conduction velocities of S and F type units in any of the muscles examined.

Relation between log maximal tetanic tension and conduction velocity of fatigue-resistant units. This relation, for the several muscles shown in Fig. 6, is similar, although its slope and its position on the conduction velocity axis differ from one muscle to another. FF units in all the muscles examined showed little or no relation between maximal tetanic tension and axonal conduction velocity.

Tension developed by motor units in different muscles. The average maximal tetanic tension developed by a given type motor unit differs from one muscle to another, as is shown in Table 5. FF units in peroneus brevis, peroneus longus, peroneus tertius, plantaris and medial gastrocnemius all developed nearly the same mean tension, namely about 40 g, and had twitch contraction times of 20–26 ms. In lumbricalis superficialis the mean tension of FF units was less (16 g) and the contraction time slightly less; this however is based on relatively few units. The FR units varied in mean maximal tetanic tension over a twofold range, being about 6–8 g in peroneus longus and tertius and lumbricalis superficialis and near 17 g in peroneus brevis, plantaris and gastrocnemius medialis. Their mean contraction times were quite similar. S units showed considerable variation in mean tetanic tension and in twitch contraction times between different muscles. Thus, there was a tenfold difference between the mean S maximal tetanic tension in lumbricalis superficialis and soleus.

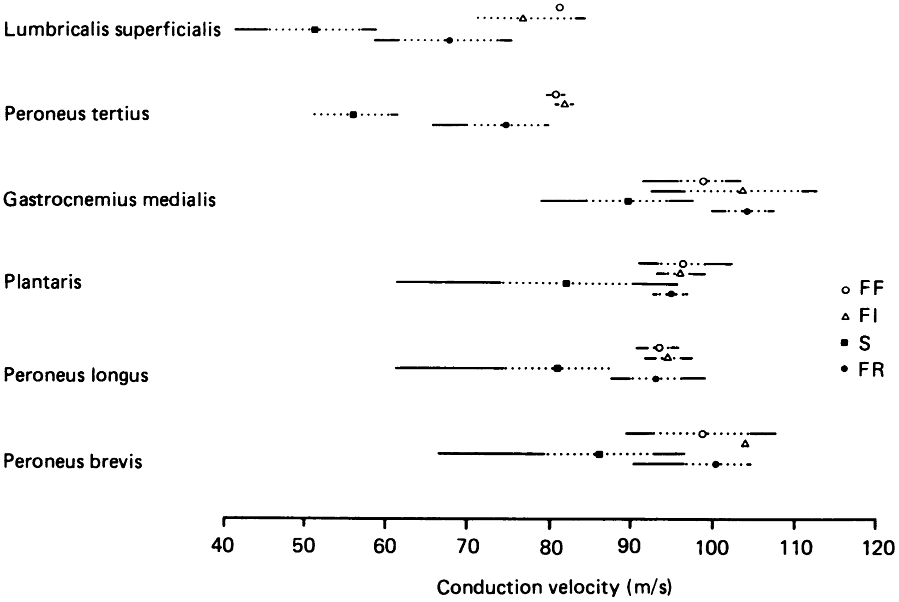

Fig. 5. Conduction velocities of motor axons to different types of motor unit in six hindlimb muscles from representative single experiments. Total width of bar indicates overall range, dotted portion one standard deviation and symbol the mean value.

Mean S contraction times ranged from about 35 (peroneus tertius and brevis) to 75 ms (soleus and gastrocnemius medialis). It is difficult to compare the tension responses of tenuissimus because of its unusual geometry (Adrian, 1925).

Figure 7 shows a comparison of the tension developed by motor units of a soleus muscle in one animal and those of plantaris in another at a stimulation frequency of 20/s, as a function of axonal conduction velocity. There are several points of interest. Although the range of conduction velocities of the soleus motor axons is appreciably slower than of those to plantaris, the tensions developed are considerably larger. The tensions developed by the plantaris units differ from those developed at a stimulation frequency of 200/s (compare with Fig. 6). The correlation between log tetanic tension and conduction velocity at 20/s is considerably poorer than at 200/s. Further, at a frequency of 20/s, which is much closer to the physiological rate of

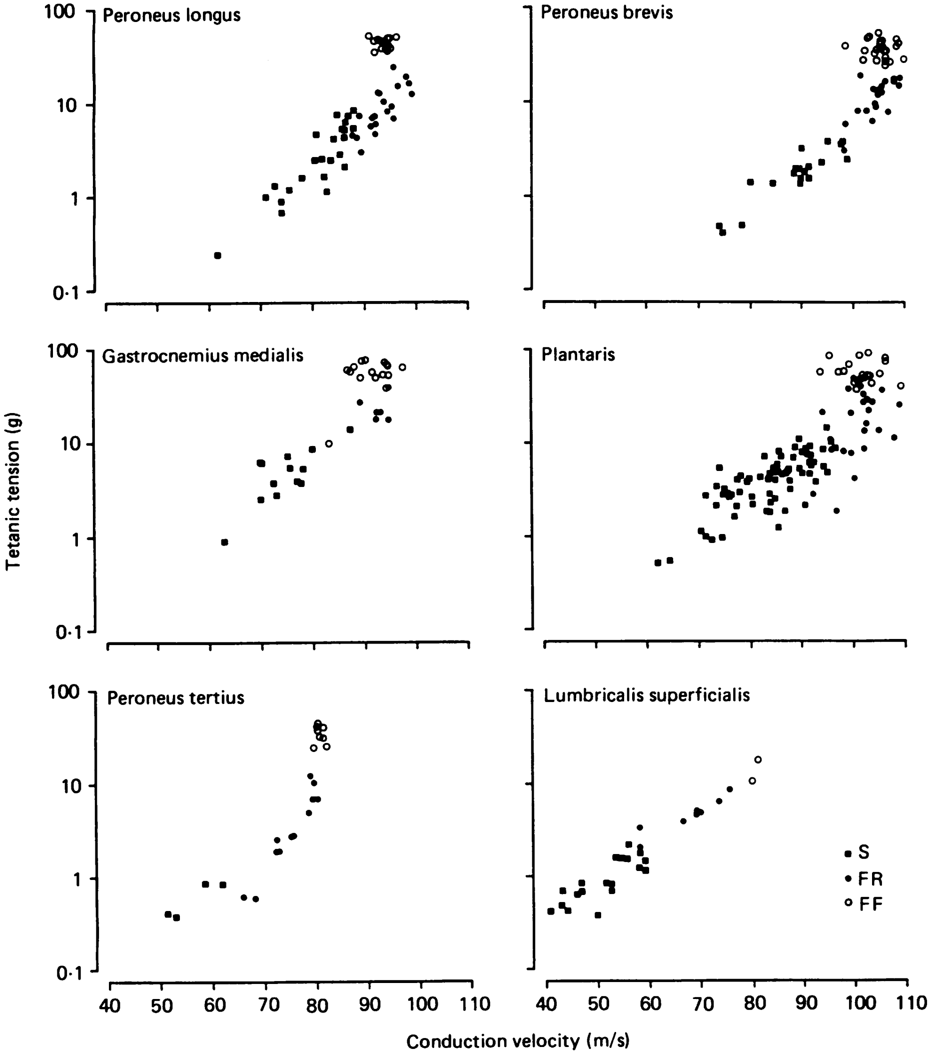

Fig. 6. Scatter plots of relation between maximal tetanic tension (200/s) and conduction velocity in S, FR and FF units in six representative individual experiments on different hindlimb muscles.

discharge, the tension developed by S units of higher conduction velocity was often greater than that developed by the slower of the FR units.

Relation between log maximal tetanic tension and conduction velocity. The correlation coefficients and *P* values of this relation, for the different types of motor unit in all the experiments, are shown in Table 4. It may be seen that for most of the muscles examined there is a high and very significant coefficient for S units and for all R units. Within the FR population there is a fairly high and probably significant positive correlation in some experiments while in others there is none. There is generally no significant correlation in the FF motor units. In spite of this, the overall

TABLE 5. Mean tetanic tensions, TT (g), and mean contraction times, CT (ms), of different types of motor unit in eight hindlimb muscles

		S		FR		FF		FI	
Muscle		Mean	±S.D.	Mean	±S.D.	Mean	±S.D.	Mean	±S.D.
P. brevis	TT	2·7	±2·1	17·2	±9·4	40·9	±16·2	33·7	±11·6
	CT	36·6	±7·3	24·1	±3·6	25·4	±4·9	23·9	±4·5
P. longus	TT	2·3	±2·0	7·2	±5·2	37·3	±13·1	17·8	±7·0
	CT	44·9	±13·4	29·5	±4·7	25·2	±4·8	23·8	±4·1
P. tertius	TT	1·3	±0·8	7·8	±4·9	39·1	±8·0	26·0	±11·0
	CT	34·4	±6·2	27·0	±4·5	26·2	±2·6	24·9	±4·9
Plantaris	TT	3·9	±2·6	17·6	±12·2	39·5	±19·5	23·3	±17·4
	CT	49·5	±16·2	25·2	±4·5	20·5	±2·7	21·9	±4·1
Soleus	TT	12·7	±5·2	—	—	—	—	—	—
	CT	75·9	±15·0	—	—	—	—	—	—
Gastroc. med.	TT	3·6	±2·6	16·9	±9·1	38·3	±17·2	23·8	±12·5
	CT	76·1	±23·1	31·5	±4·9	27·5	±5·1	29·3	±6·8
Lumbr. sup.	TT	1·4	±0·8	6·3	±4·1	16·0	±2·9	9·9	±4·1
	CT	46·1	±10·4	24·6	±4·4	17·7	±3·2	21·8	±3·1
Tenuissimus	TT	0·6	±0·5	0·9	±0·5	2·3	±1·1	1·1	±0·4
	CT	50·4	±7·2	28·9	±5·1	25·6	±2·3	24·9	±2·1

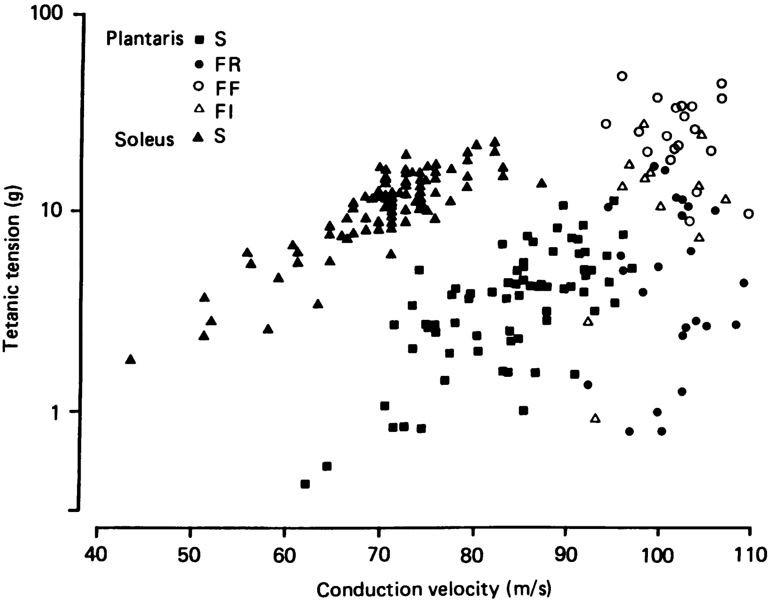

Fig. 7. A comparison of the relation between tetanic tension and conduction velocity for motor units of one experiment on soleus and one on plantaris, at a stimulation frequency of 20/s.

population shows a high correlation. It may also be seen that where there is a high correlation in individual experiments, the pooled data from a number of experiments shows a less good correlation. Of the muscles studied, the relation between maximal tetanic tension and axonal conduction velocity is most clearly seen in lumbricalis superficialis and peroneus brevis. The relation is least clear in the frequently studied gastrocnemius medialis.

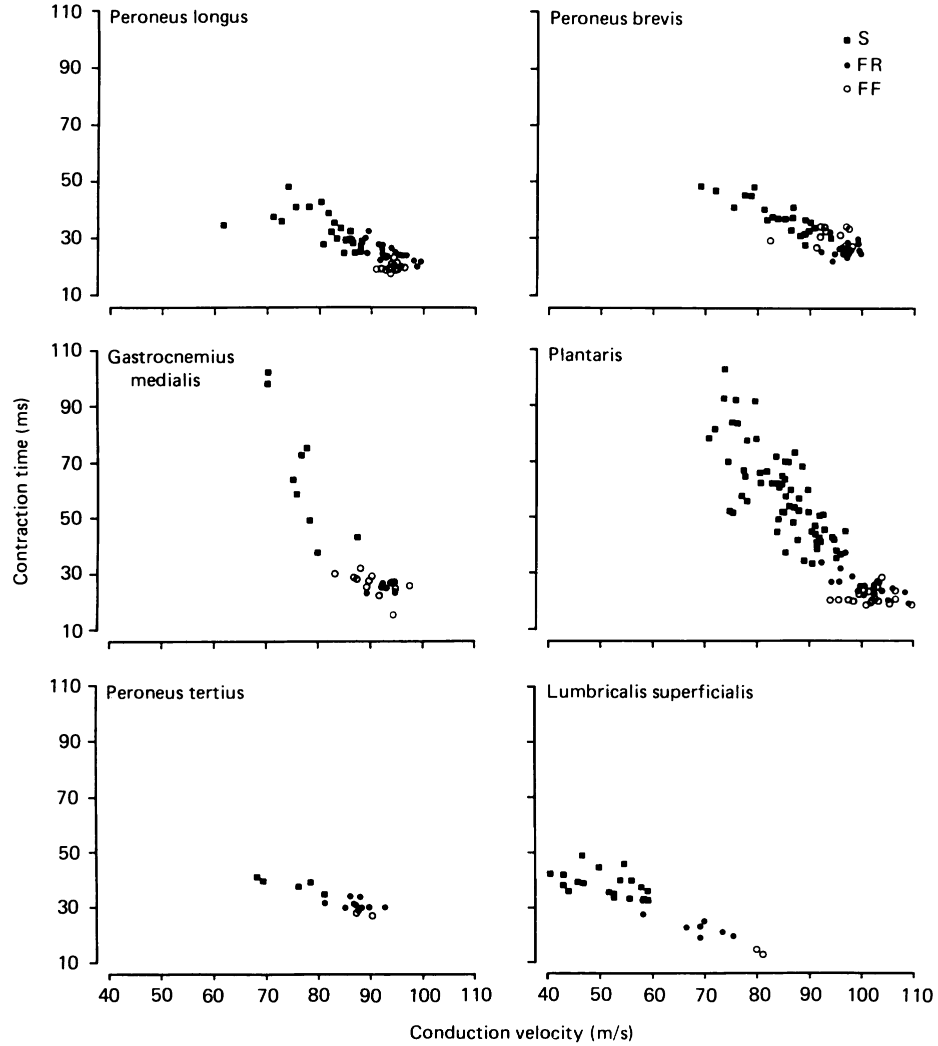

Fig. 8. Scatter plots of the relation between isometric twitch contraction time and conduction velocity of S, FR and FF units in six representative individual experiments on different hindlimb muscles.

Relationship between twitch contraction time and conduction velocity. As may be seen in the examples shown in Fig. 8, this relationship was generally similar from one muscle to another. However, the contraction times for motor units of the same type and with the same axonal conduction velocity may differ considerably from one muscle to another. For example, the S units of gastrocnemius medialis and plantaris with slow axonal conduction velocity (lower than 80 m/s) have much longer contraction times than S units of similar conduction velocities in other muscles.

DISCUSSION

The present study shows that peroneus brevis is a muscle with a high proportion of fatigue-resistant units. Our data on other muscles which have previously been studied reveal some differences. In gastrocnemius medialis we found a lower proportion of FR units (16%) than in other reports (27·4%, Burke *et al.* 1973; 34·8%, Proske & Waite, 1974; 28%, Reinking *et al.* 1975). One reason is that our fatigue test classified some units as FI which would be FR by the criteria of Burke, Levine, Tsairis & Zajac (1973) (see Methods). It should also be pointed out that some of the units classified as FI because the response fell to slightly below 0·75 of the maximum at the 2 min interval showed little or no further decline during the remainder of the fatigue test and the absence of late fatigability made them more similar to FR units. Such units were also like FR units in developing less tension than typical FI units. The proportion of the different types of motor units observed in peroneus tertius is quite similar to those reported by Jami *et al.* (1982): S, 22%, FR, 39% and FF, 30%. Among the other muscles (peroneus brevis, plantaris and lumbricalis superficialis) we found that the proportion of S units is $\frac{1}{2}$ or more of the total population. Those muscles with lower percentages of S units, such as peroneus tertius, have correspondingly higher fractions of FR units, so that the total population of fatigue-resistant units (R units) is often $\frac{2}{3}$ of the motor pool.

Within the S and FR populations (R units), the tetanic tension produced by a motor unit shows a strong and highly significant positive correlation with axonal conduction velocity. Proske & Waite (1976) found such a correlation in S units but it was not significant in their sample of FR units. The present results suggest that there is probably also a significant correlation in FR units although the limited range of conduction velocities of FR axons and the uncertainties in determining the values of conduction velocity make this difficult to demonstrate. The lack of a discontinuity in the tensions developed by the more rapidly conducting S units and the more slowly conducting FR units suggests that the total fatigue-resistant population may be a functional continuum.

Factors that determine the tension developed by a motor unit are the number of muscle fibres innervated by the motor axon (the innervation ratio), their cross-sectional area, and their intrinsic contractile characteristics. The latter depend not only on the particular composition of their contractile proteins, myosin and actin, but also on the factors that control their interaction, such as the rates of release and uptake of cytoplasmic Ca^{2+} from the sarcoplasmic reticulum. In spite of the many studies on this question, there is no definitive evidence as to which factors are responsible for the striking relationship between maximal tetanic tension and axonal conduction velocity in R units.

Burke & Tsairis (1973) calculated the innervation ratio for the different types of gastrocnemius medialis units of cat using the glycogen-depletion technique and considered their results to cast doubt on the assumption that the relation between contractile response and conduction velocity was due principally to variation in the innervation ratio as a function of axonal diameter. In their study, muscle fibre cross-sectional area appeared to be a significant factor. They proposed that the specific tension per cross-sectional area of the muscle fibres was most important. While their data certainly indicate that the differences in contractile responses between motor units of different types cannot be attributed only to differences in innervation ratios, they do not preclude a relationship between axonal conduction velocity and innervation ratio within the S or FR groups.

The negative correlation between contraction time and axonal conduction velocity within the fatigue-resistant population might be taken to indicate that there is a gradation of contractile properties in these motor units related to motor axon size. This would suggest that the size of the motor axon, or its related activity, may determine the composition of the contractile proteins and/or the control of Ca^{2+} release and uptake in the muscle fibres it innervates. If this were true, S muscle fibres would not be a uniform population but graded in their properties and this might hold for the FR population as well. Such a gradation in properties might explain, at least in part, the development of lower tension in motor units of the more slowly conducting axons.

If the relation between tetanic tension of S units and the conduction velocity of their motor axons does not reflect a wide range of contractile properties for type I (SO, slow oxidative) muscle fibres, it must be due to other factors such as a variation in the number and/or diameter of muscle fibres innervated by an axon as a function of its size, each muscle fibre having similar contractile properties (Proske & Waite, 1974). There could be in fatigue-resistant units a logarithmic relation between axonal size and number of muscle fibres innervated. One possible basis for this might be as follows: if each such motor axon made a series of dichotomous divisions, the number of which depended on axonal diameter, the number of muscle fibres innervated could be logarithmically related to axonal size.

Indirect evidence that innervation ratios may differ for the several motor unit types comes from the comparison between the proportion of FR and S units with the percentage of the associated histochemical fibre types, respectively fast oxidative glycolytic, FOG, and slow oxidative, SO (Ariano, Armstrong & Edgerton, 1973). In plantaris, peroneus longus and brevis, the percentages of S units was considerably higher (52, 44 and 33 respectively) than the percentage of SO fibres (26, 20 and 6), while the proportions of FR units and FOG fibres were similar.

Whatever its basis, the relation between tension developed by a motor unit and its axonal conduction velocity has important physiological consequences. Within the fatigue-resistant population, viewing S and FR units as a continuum, the motoneurones associated with the more slowly conducting axons, being smaller in size, may be expected to be recruited first according to the size principle (Henneman, Somjen & Carpenter, 1965). From the relation between maximal tetanic tension and conduction velocity one would expect additional motoneurones to be recruited in an order associated with increasing increments of tension response. However, at more physiological discharge rates the tension increments associated with recruitment of FR units may actually be less than those associated with the most rapidly conducting S units (see Results, Fig. 7).

The axonal conduction velocities of FF motor units overlap nearly completely with those of FR units. If recruitment occurred strictly on the basis of motoneurone size and hence on axonal diameter, as indicated by Bawa, Binder, Ruenzel & Henneman (1984), after the recruitment of S units a mixture of FF and FR units would be recruited. Bawa *et al.* (1984) did not examine motor unit types but found very few exceptions to a recruitment order strictly on the basis of ascending axonal conduction velocity in both soleus and the composite muscle, gastrocnemius medialis. However, it seems that a rigid order of recruitment based on motoneurone size alone is not always followed. Zajac & Faden (1985) investigated the recruitment order of type-identified motor units and found that FF units had a higher threshold for recruitment in a number of reflex actions than FR units. They compared the thresholds of motor units of various types in plantaris muscle of cat by examining responses to monosynaptic excitation produced by stretch or by electrical stimulation, in ventral root filaments in continuity. A comparison of pairs of motoneurones showed that the threshold for recruitment followed the sequence: S < FR < FI < FF.

Recruitment order may also vary in different reflex actions. Kernell & Sjöholm (1975) found that the order of recruitment of motor units in the first lumbricalis profondus muscle of the cat's foot was often different in response to pinching the foot and in response to cortical stimulation (see also Kernell *et al.* 1975). Mizote (1982) showed that the recruitment order of motor units to this muscle following cortical stimulation could be altered in a reversible manner by stimulation of the digital nerve and that such alteration could persist for several minutes following digital nerve stimulation.

It seems clear that recruitment order is, to a large extent, determined by motoneurone size and hence related to axonal conduction velocity but other modifiable factors can alter that order. In the case of fatigue-resistant units, the smooth progression in size of tension increments as larger and larger axons are brought into play is of fundamental importance.

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