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Distribution of Physiological Types of Motor Units in the Cat Peroneus Tertius Muscle*

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Summary. Motor units of the cat peroneus tertius muscle were systematically analyzed using the criteria established by Burke et al. (1973). On the basis of their speed of contraction and resistance to fatigue, 121 (97%) of 125 motor units examined in ten adult cats could be classified as belonging to one of four types: fast-fatiguable (FF), fast-resistant (FR), fast-intermediate (FI), and slow-resistant (S).

Peroneus tertius was found to contain 30% FF motor units, 9% FI units, 39% FR units, and 22% S units. Contraction times of fast motor units (FF, FR, and FI) ranged from 15 to 27 ms and those of S units from 26 to 42 ms. The mean tetanic tensions were 37 g for FF units, 29 g for FI units, 7.5 g for FR units, and 1.1 g for S units.

Fast motor units displayed considerable post-tetanic potentiation of twitch tension. Under similar conditions of stimulation, FF units appeared able to potentiate more and faster than FR units.

Key words: Motor unit types – Twitch and tetanic tensions – Potentiation – Peroneus tertius muscle – Cat

Introduction

The cat peroneus tertius (also termed peroneus digiti quinti) is a small muscle whose function is extension and abduction of the fifth digit and also flexion of the foot. It contains about 30 motor units (Barker et al. 1970) with a relatively high incidence of skeleto-fusimotor (or β) innervation: in a sample of 114 peroneus tertius motor units, we found 36 (31%) β units, i.e., motor units including intra- and extrafusal muscle fibers (Jami et al. 1980, 1982). On the basis of the criteria established by Burke et al. (1973), 17 (47%) of these β motor units were identified as fast-contracting and resistant to fatigue (FR units), six (17%) were fast-contracting and fatiguable (FF units), and 13 (36%) were of the slow-contracting and fatigue-resistant type (S units). It was not known, however, whether these proportions corresponded to the distribution of the different types of motor unit in the muscle. The present paper reports a study of peroneus tertius motor units using the criteria of Burke et al. for identifying their type. As in other muscles (Burke et al. 1973; Proske and Waite 1974; Dum and Kennedy 1980; Mc Donagh et al. 1980) these criteria were found to allow unequivocal classification of nearly all peroneus tertius motor units either in one of the three main types (FF, FR, and S) or in a fourth type termed fast-intermediate (FI) because it includes fast-contracting units with fatiguability intermediate between those of FF and FR types (Burke et al. 1973; Stephens et al. 1973; Hammarberg and Kellerth 1975; Goslow et al. 1977; Dum and Kennedy 1980; Mc Donagh et al. 1980).

Material and Methods

Adult cats (2–3.5 kg) were anesthetized with an initial i.p. dose of 45 mg/kg pentobarbitone sodium; the level of anesthesia was subsequently maintained by i.v. injections of the drug. Blood pressure was monitored, and body temperature was maintained at 38° C. The vertebral column and left hind limb were rigidly fixed. The L6 to S1 ventral roots were exposed and cut near their exit from the spinal cord. All the hip, tail, and hind limb muscles were denervated except the peroneus tertius.

The muscle and its tendon were freed without damaging their blood supply and the tendon was firmly tied to a rigid metal ring attached to a tension transducer (Kulite strain gauge with a compliance of 160 μm per 300 g, i.e., the full range of the gauge).

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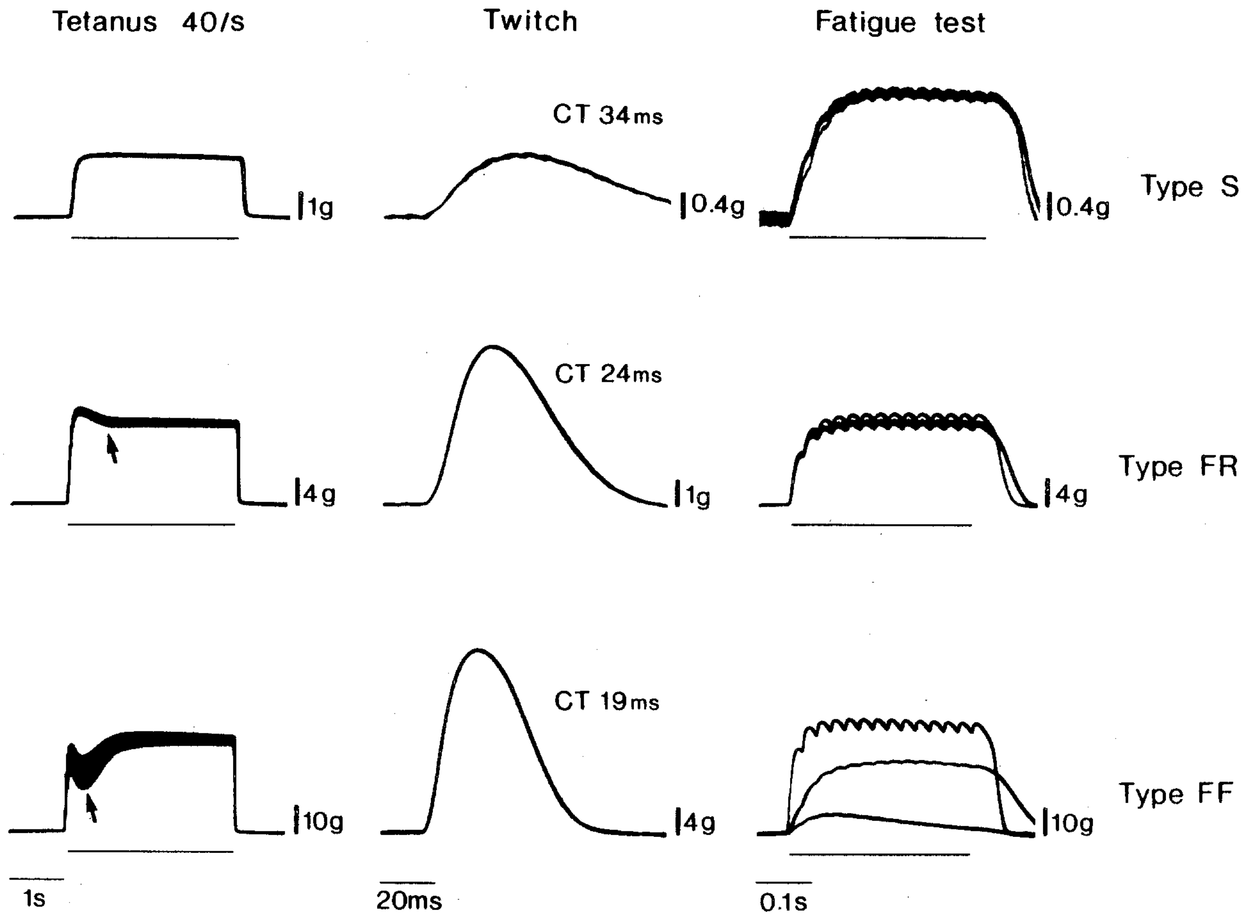

Fig. 1. Identification of motor unit type by physiological criteria. Each row shows the responses of a motor unit to the three tests used for identifying its type (see text). The three units were examined in the same experiment. All the graphs are isometric tension recorded at the muscle tendon. In first and third columns the duration of stimulation at 40/s is indicated by horizontal bars. In the graphs of first column, arrows point to the "sag". In second column CT is the contraction time. Twitch tensions were 26 g, 5.7 g, and 0.8 g for the FF, FR, and S units, respectively. The fatigue tests are represented by superimposed records of first, 60th, and 120th tetanus. The conduction velocities of the axons innervating the FF, FR, and S units were 102 m/s, 97 m/s, and 85 m/s, respectively

The length of tendon between muscle and ring was kept as short as possible, and the natural direction of pull of the muscle was maintained. The muscle was held at the length for which it produced maximal twitches.

The nerve to peroneus tertius was dissected over 10–15 mm and mounted on a recording electrode. The second electrode was placed in contact with the preparation at some distance from the muscle so that nerve and muscle potentials elicited by the stimulation of motor axons in ventral roots could be recorded through the same amplifier. In addition, to check whether any changes in the size of muscle action potentials accompanied changes in motor unit tension, the muscle action potentials were separately recorded with either a pair of fine flexible tungsten wire electrodes hooked 1 cm apart in the muscle fascia or/and a pair of silver-ball electrodes placed on adjoining muscles so that they were not displaced during contraction of peroneus tertius motor units. The exposed areas of the spinal cord and of the hind limb were covered with pools of mineral oil maintained at body temperature.

Single motor axons were isolated by splitting ventral roots until stimulation of a filament elicited an all-or-none action potential in the muscle nerve together with an all-or-none muscle action potential of the motor unit. Stimulation rates of 20–30/s were used during this procedure, care being taken to reduce as far as possible the amount of stimulation applied to each motor unit. In addition, at least 1 h was allowed for each motor unit to recover from possible fatigue caused by repeated stimulation during isolation. The motor units were then submitted to several tests in the following order: (1) single shock stimulation eliciting an initial twitch response that will be referred to as "twitch *a*"; (2) 3 s period of stimulation at 40/s (Fig. 1, first column). In peroneus tertius, 75% of motor units innervated by axons with conduction velocities between 70 and 110 m/s display unfused tetanic contraction during stimulation at 40/s, whereas the contraction of motor units innervated by slower axons appears fused; (3) single shock stimulation producing a "twitch *b*" response (Fig. 1, second column). As "twitch *a*" was not recorded in all experiments, the twitch tension and contraction time of each motor unit were measured on the "twitch *b*" response, with consequences that will be discussed below; (4) 0.5 s period of stimulation at 200/s giving maximum tetanic response; (5) stimulus trains of 330 ms duration and 40/s rate repeated every second were used to determine the fatiguability of the motor unit. To begin with, stimulus trains were repeated until the motor unit response reached a maximum. Then, 120 trains were delivered in 2 min, and the fatigue index was defined as the ratio of the maximum tension produced during the 120th tetanus to that produced during the first of this series (Fig. 1, third column). FF units have fatigue indices below 0.25 while FR and S units have fatigue indices of 0.75 and above. The fatigue indices of FI units range between 0.25 and 0.75 (Burke et al. 1973).

Results

Tension Responses During Unfused Tetanic Contraction

In addition to the twitch contraction time and the fatigue index, a third criterion is necessary to allow unambiguous identification of motor unit types because, even though the fatigue test readily distinguishes type FF from the other types, the ranges of contraction times are not the same in all muscles and the limit between fast and slow contraction is not absolutely clear-cut. Burke et al. (1973) have proposed using as an additional criterion the shape of the tension response of a motor unit during unfused tetanic contraction. The responses of fast-contracting motor units – FF, FI, and FR units – to stimulation at 40/s display an early tension maximum reached after the first three to six stimuli and followed by a slight decline or "sag" in tension (Fig. 1, first column). This property has been shown to be intrinsic to active muscle fibres and not due to any pre- or post-synaptic effect at the neuromuscular junction (Burke et al. 1976a). The "sag" is not seen in type S units unless stimulation frequencies below 5/s are used. Its presence or absence in the tension response to stimulation at 30–40/s is therefore used as a complementary criterion for distinguishing fast- from slow-contracting motor units (Burke et al. 1973).

In the response of the FF unit illustrated in Fig. 1 (first column) the sag was followed by an increase in tension leading to a plateau whose level was slightly above that of the initial peak, whereas in the response of the FR unit there was no increase in tension subsequent to the sag. Both shapes of response were observed among FF as well as FR units, although the time course of the sag was usually slower in the responses of FR units than in those of FF units. FF units sometimes displayed relatively large increases in tension during stimulation at 40/s. Potentiation of tension during unfused tetanic contraction is known to occur in whole muscles (Euler and Swank 1940; Bowman et al. 1962). In single motor units of cat lumbrical muscles, Kernell et al. (1975) similarly observed that stimulation at 42/s induced a progressive increase of tension for some fast-contracting units but not for the slow ones. In the present study, potentiation of tension during 40/s stimulation was observed only in the responses of motor units that had been left "to rest" (i.e., not stimulated) for about 1 h. Upon repetition of stimulation trains, the shape of the response changed, displaying an initial peak of tension followed by a sag after which the tension would slowly decline, as illustrated in Fig. 2. However, the change affected essentially the early part of the response and after 3 s of stimulation the level of tension was approximately the same in the first and second responses. For unknown reasons, the responses to first stimulation of some apparently "rested" FF and FR units displayed the same shape as the responses to second stimulation shown in Fig. 2 (see for instance the FR unit in Fig. 1).

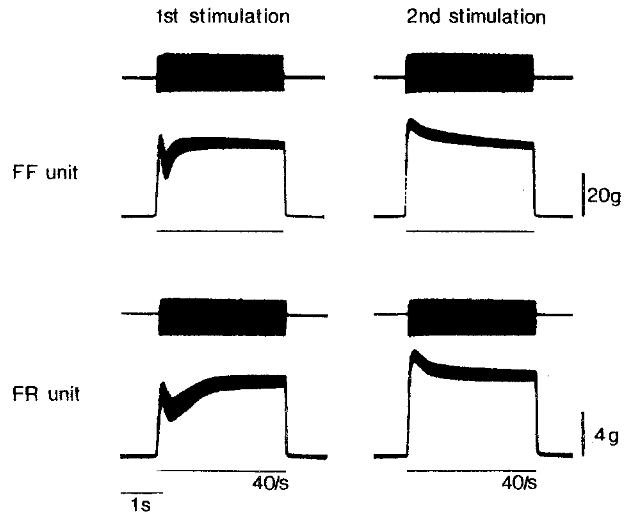

Fig. 2. Responses of FF and FR units to two successive trains of stimulation at 40/s. Muscle action potentials (*upper line*) and isometric tension (*lower line*) were recorded simultaneously. Two motor units from the same experiment. Conduction velocity of motor axons: 96 m/s for the FF unit and 91 m/s for the FR unit. The first stimulation was applied after the units had been left without stimulation for 1 h and the second stimulation followed immediately. Note the absence of any change of muscle action potentials in the responses of both units to first and second stimulation

Classification of Motor Units

The FF unit of Fig. 1 was unequivocally identified by the conjunction of three criteria, i.e., presence of a sag in the tension response to 40/s stimulation, relatively brief contraction time (19 ms) and low fatigue index (0.18). The FR unit also displayed a sag but its fatigue index was high (0.9) whereas the S unit, with an equally high fatigue index (1) showed no sag and had a relatively long contraction time (34 ms). Using these criteria, 121 (97%) of 125 motor units examined in 10 experiments could be identified as either FF, FI, FR, or S units (Fig. 3). FI units had

Table 1. Physiological properties of peroneus tertius motor units

	Conduction velocity of motor axon (m/s)	Twitch contraction time (ms)	Fatigue index	Twitch tension (g)	Tetanic tension (g)
FF	85–110.5 n = 36	15–22 (18.5±1.5) n = 36	0–0.24 (0.10±0.05) n = 36	5.5–37.3 (16±8.5) n = 26	16.2–62 (37±12) n = 17
FI	90–103.5 n = 11	17–26 (20.5±3) n = 11	0.26–0.65 (0.40±0.1) n = 11	2.3–22.1 (8.4±6.5) n = 9	13.5–48 (29±13) n = 5
FR	79–105 n = 47	17–27 (21.5±3) n = 47	0.76–1 (0.90±0.05) n = 47	0.2–12.9 (2.4±2.4) n = 40	0.8–26 (7.5±7) n = 24
S	57.5–97.5 n = 27	26–42 (32±4.5) n = 27	0.91–1 (0.95±0.05) n = 27	0.1–3.7 (0.7±0.9) n = 22	0.3–4.5 (1.1±0.6) n = 11

Values are ranges found for each sample; figures in parentheses are means ± SD; n gives the size of the sample

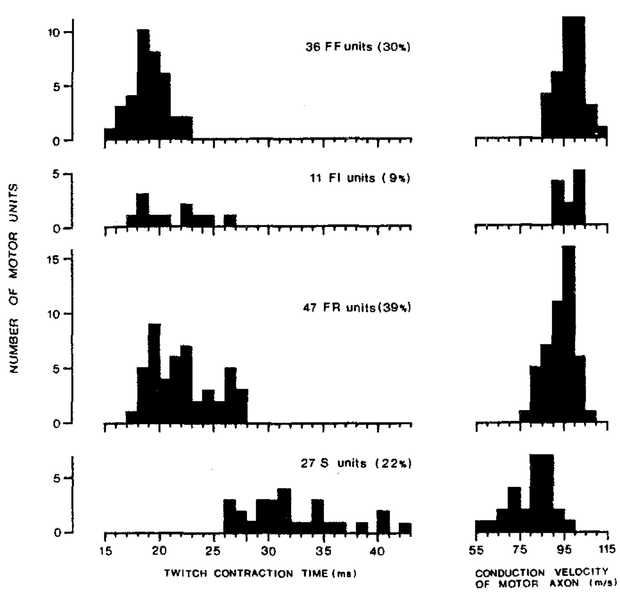

Fig. 3. Histograms of twitch contraction times and conduction velocities of motor axons of 121 motor units examined in ten experiments

contraction times in the same range as FF and FR units and displayed sags in their responses to 40/s stimulation, but their fatigue indices had intermediate values between 0.25 and 0.75. The four units that could not be identified were found in two experiments. They displayed aberrant conjunctions of characteristics, such as a long contraction time associated with a sag and/or a low fatigue index.

The physiological properties of peroneus tertius motor units are summarized in Table 1 and the proportion of motor units of each type is given in Fig. 3, showing for each group the distribution of twitch contraction times and conduction velocities of motor axons. The contraction times of FF and S units are clearly separated whereas some overlap occurs between FR and S units, which justifies resorting to the sag criterion for separating these two groups, since their fatigue indices also are in the same range. There is much more overlap in conduction velocities of motor axons innervating the four types of motor units, so that the range between 85 and 100 m/s – which makes up over one half of peroneus tertius population – includes units of each type.

The fatigue indices were distributed as follows within each type of motor unit: all the FF units except two had a fatigue index below 0.20 and for two thirds of them it was below 0.10; all the FR units except four had a fatigue index above 0.80 and for two thirds of them it was above 0.90; among the FI units, seven had fatigue indices ranging between 0.40 and 0.65 and four had indices between 0.26 and 0.35; finally, all the S units had fatigue indices ranging between 0.90 and 1. Muscle action potentials were monitored throughout fatigue tests in order to verify that they remained unaffected. Muscle potentials of S and FR units (mostly small units, see below) did not change during the test, whereas those of the largest FF units were sometimes seen to subside very quickly. The reduction was meaningless, however, since it was seen mainly when the muscle action potentials were led from electrodes hooked in the muscle fascia where they could be influenced by mechanical artefacts resulting from the contraction of these big motor units. Simultaneous recording with more distant electrodes showed little or no change in muscle action potentials of the same units during fatigue tests.

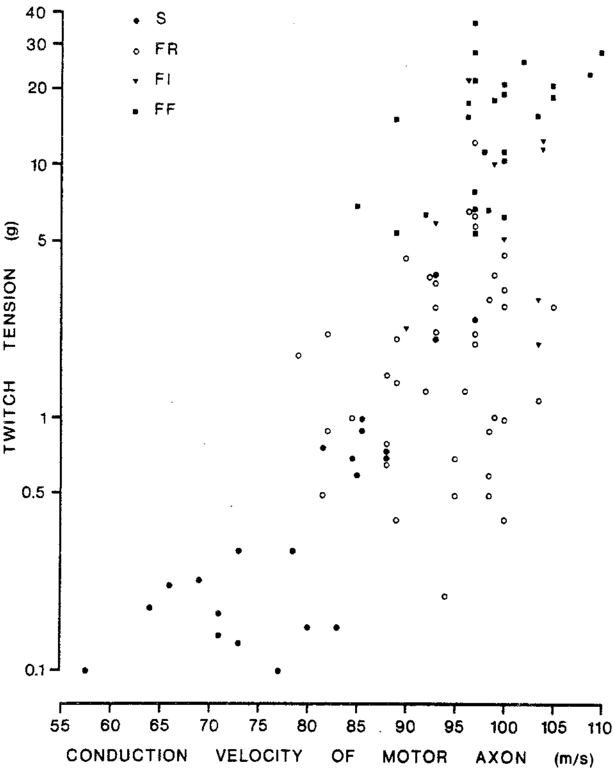

Fig. 4. Twitch tensions of 97 motor units (22 S, 40 FR, 9 FI, and 26 FF) examined in eight experiments. This sample is included in the sample of Fig. 3

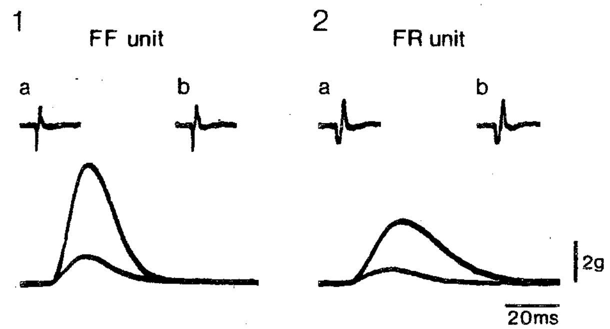

Fig. 5. Potentiation of twitch tension by stimulation at 40/s for 3 s. Two motor units from the same experiment. Twitches *a* and *b* have been superimposed. Insets show the muscle action potential recorded with each twitch. For the FF unit (1), twitch tension was 1.5 g and 6 g for *a* and *b*, respectively, and for the FR unit (2) it was 0.9 g and 3 g for *a* and *b*, respectively. Conduction velocities of motor axons: 89 m/s for the FF unit and 90 m/s for the FR unit

Twitch Tensions and Potentiation

The tensions developed during a twitch by 97 peroneus tertius motor units are plotted in Fig. 4 with logarithmic ordinates against the conduction velocities of their motor axons. Motor units innervated by axons with relatively slow conduction velocities tended to develop less tension than units innervated by faster axons but there was no precise correlation between twitch tension and axonal conduction velocity similar to that observed in lumbrical muscles by Bessou et al. (1963). Twitch tensions varied over a wide range (from 0.1 to 37.3 g) with one half of S units developing less than 0.5 g and two thirds of FF units developing more than 10 g (cf. Wuerker et al. 1965). Among the units innervated by axons conducting at 90 m/s and faster, the FR group, with nearly all units developing less than 5 g, appeared clearly separated from the FF group in which all tensions were above this value.

The difference between fast and slow motor unit twitches has been somewhat enhanced in the present sample because twitch *b* responses were measured rather than twitch *a*. As stated in the Methods section, twitch *a* was recorded after the motor unit had been left without stimulation for at least 1 h whereas twitch *b* was recorded immediately after stimulation at 40/s had been applied for 3 s to the motor unit. Although this amounts to much less stimulation than the regimes usually applied to produce fully potentiated twitches (cf. Olson and Swett 1971; Burke et al. 1973; Kernell et al. 1975) such stimulation proved enough to elicit appreciable potentiation in the twitch tension of FF, FI, and FR units. In the instance illustrated by Fig. 5, the FF unit displayed a four-fold increase in tension from twitch *a* to twitch *b* (without any change in muscle action potentials) together with a slight lengthening of contraction time (13 and 15 ms for *a* and *b*, respectively) and of half-relaxation time. For the FR unit of Fig. 5, the increase in tension was about three-fold while contraction time lengthened from 15 to 19.5 ms and relaxation also slowed down. For both FF and FR units, restoration of initial twitch parameters took place within 10–15 min (cf. Olson and Swett 1971). In a sample of 47 FF units (from nine experiments) the tension ratios of twitch *b* to twitch *a* (potentiation ratios) had a mean value of 4.1 ± 1.9 (range 1–9.3) and the increase in contraction time averaged 1 ms. In a parallel sample of 45 FR units (from the same experiments) the mean of potentiation ratios was 2.6 ± 1.1 (range 0.9–5.8) and the average increase in contraction time was 2.8 ms. Variance analysis showed that the differences between FF and FR units were highly significant ($p < 0.001$), which means that FF units are more apt than FR units to develop potentiation after a given amount of stimulation, i.e., here a train of 3 s at 40/s. Under the same conditions most S units did not display potentiation of twitch tension and for those which did, the potentiation ratio remained quite low (range 1.1–1.3) while contraction times did not

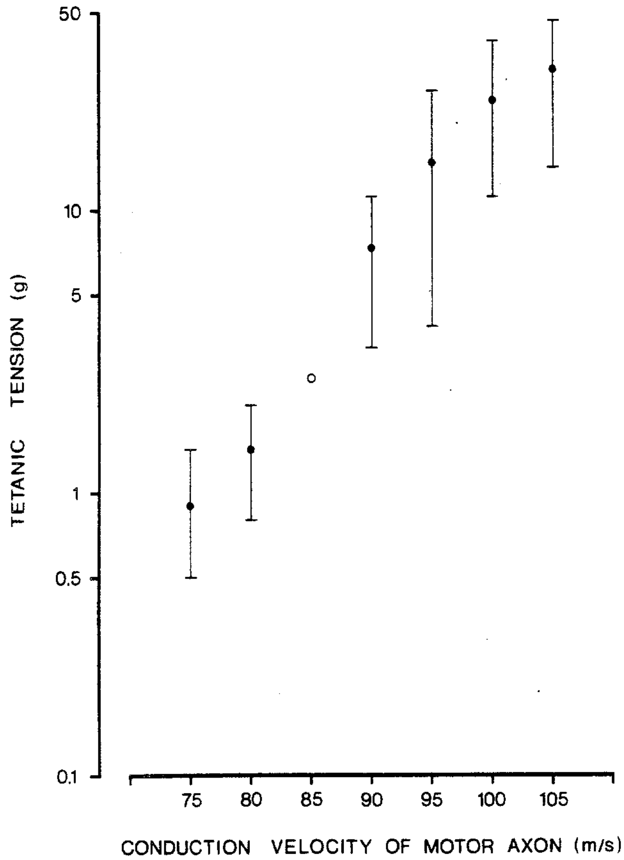

Fig. 6. Relation between the logarithm of tetanic tensions developed by 57 motor units and the conduction velocities of their motor axons (see text). The dots on vertical bars indicate mean value of tension ± SD. The open circle represents the tetanic tension of a single unit

change. In the sample studied by Kernell et al. (1975), the most "potentiation-prone" motor units also appeared to be the less resistant to fatigue.

Maximal post-tetanic potentiation is usually produced by high-frequency stimulation. It was examined in the present study for a limited number of motor units, following the procedure used by Burke et al. (1973), i.e., stimulation at 200/s during 0.5 s and followed after 3 s by a single shock, the sequence being repeated after an interval of 3 s until the response to the single shock had reached a maximum. It took four to ten such sequences to produce maximally potentiated twitches and those of fast units developed of course more tension than twitches recorded after 3 s of stimulation at 40/s. Again, FF units tended to potentiate more and faster than FR units. Type S units showed much weaker signs of potentiation, but neither did they appear depressed as was observed in other muscles (Bagust et al. 1974; Kernell et al. 1975).

Tetanic Tensions

The tetanic tensions of 57 peroneus tertius motor units examined in four experiments were found to range from 0.3 to 62 g. Their axonal conduction velocities (75–107 m/s) were grouped in classes of 5 m/s intervals and for each class the mean and S.D. of the corresponding tetanic tension were plotted against conduction velocity (Fig. 6). As previously observed in other muscles (Bagust et al. 1973; Jami and Petit 1975) an approximately linear relation appears between the logarithm of tetanic tension developed by motor units and the conduction velocity of their axon (cf. also Mc Phedran et al. 1965; Wuerker et al. 1965; Olson and Swett 1966; Appelberg and Emonet-Dénand 1967; Emonet-Dénand et al. 1971; Proske and Waite 1974, 1976). In the upper range of conduction velocities, however, the mean tetanic tensions are slightly smaller than would be expected from a strictly linear gradient. This might be due to the fact that motor units of all types have been pooled according to their axonal conduction velocities whereas the ranges of tetanic tensions are quite different for each type (cf. Table 1). For instance, the class of 100–104 m/s, with a mean tetanic tension of 24.8 ± 14 g, includes 7 FR, 4 FI, and 8 FF units for which the mean tetanic tensions were 9.5 g, 27.8 g, and 45.8 g, respectively. In the whole sample, the mean tetanic tensions of the motor units of each type were 37 ± 12 g for FF units, 29 ± 13 g for FI units, 7.5 ± 7 g for FR units, and 1.1 ± 0.6 g for S units. Considering that the total population of peroneus tertius includes about 30 motor units (Barker et al. 1970) of which 30% are FF, 9% FI, 39% FR, and 22% S (Fig. 3), it follows from the above figures that FF units could account for as much as two thirds of the total muscle tetanic tension whereas FR units would produce less than 20% of this tension and S units less than 2%; the few FI units present in the muscle might develop nearly as much tetanic tension as the FR group. The fact that fatiguable motor units produce most of peroneus tertius tension might account for the low fatigue index (ca. 0.30) of the whole muscle (Zytnicki, unpubl. data).

Discussion

It could be expected to find the three main types of motor units in the cat peroneus tertius, since this muscle is known to contain three types of muscle fibers, i.e., 45% fast-glycolytic fibers (FG, corresponding to FF units), 45% fast-oxidative-glycolytic fibers (FOG, corresponding to FR units), and 10% slow-oxidative fibers (SO, corresponding to S units)

(Ariano et al. 1973). The latter figure suggests that S units are appreciably smaller than units of other types since they make up 22% of the motor unit population with only 10% of the fiber population.

Although their functional significance is not yet clearly established, motor units of the FI type have been found in all the cat muscles examined so far. Interconversions from FF to FR type have been considered to occur as a result of training and exercise (Burke and Edgerton 1975) and FI units might represent a transitional stage. There might also exist permanent variants of the main FF and FR types of motor units. Whatever may be the case, and provided similar tests are applied, the proportion of FI units appears to be fairly constant, that is 7.5% in tibialis anterior, 9% in extensor digitorum longus (Dum and Kennedy 1980), 8% in tibialis posterior (Mc Donagh et al. 1980) and 9% in the present sample; for medial gastrocnemius, Burke and coworkers first reported only 2.5% FI units (1973) but in a later study they found 8.4% (Burke et al. 1976b) and in the sample studied by Proske and Waite (1974) there were about 10% motor units displaying fatigue resistance intermediate between those of FF and FR units. The resistance to fatigue displayed by a motor unit is correlated with the oxidative enzyme activity of its muscle fibers. Fibers composing FR or S units have high activity while in fibers of FF units the activity is low and in fibers of FI units it is intermediate (Burke et al. 1973; Hammarberg and Kellerth 1975; Dum and Kennedy 1980; Mc Donagh et al. 1980). Surprisingly, there is no specific histochemical profile corresponding to the fibers of FI units in the two main classification schemes that are currently applied in histochemical studies of muscle. In their extensive investigation, Ariano et al. (1973) examined 33 different hindlimb muscles of five mammals, including the cat. On the basis of myosin ATPase activity (correlated with the speed of contraction) and oxidative enzymes activities, they distinguished only three types of fibers, i.e., the SO, FG, and FOG types that have been mentioned above. With the other identification procedure widely used in human and animal studies, four types of fibers are demonstrable on the basis of the histochemical reaction of ATPase and the pH lability of this reaction. The fiber types are called 1, 2A, 2B, and 2C of which the first three clearly correspond to SO, FOG, and FG fibers, respectively (Dubowitz and Brooke 1973), but the histochemical profile of 2C fibers does not account for the physiological properties of FI units, because the oxidative enzyme activity of these fibers is very strong, almost as strong as that of type 1 fibers. In the sample of Burke et al. (1973) there was one "unclassified" unit (such units were later termed fast-intermediate) with ATPase reactions of 2B type, whereas its oxidative enzymes activity was of 2A type. However, in his study of the cat gastrocnemius, soleus, and tibialis anterior muscles, Hammarberg (1974) identified four types of fibers on the basis of their lipids and oxidative enzyme content. One of these types (called type 2 in his terminology) did exhibit staining patterns that were intermediate between those of the types corresponding to fibers of FF and FR units (see further discussion of this point in the recent review by Burke 1981).

Among the β motor units of peroneus tertius, nearly one half are of the FR type and over one third are of the S type (Jami et al. 1982). Clearly, these proportions do not correspond to the distribution of the different motor unit types in the muscle. Other factors than the proportion of a given type of motor unit may determine the incidence of β units within this type. Slow β units are innervated by axons exerting dynamic actions on spindles and their intrafusal portion is made of bag_1 muscle fibers (Barker et al. 1977) whereas β axons innervating FR units are static and the intrafusal portion of their motor unit is chiefly made of chain fibers (Harker et al. 1977). The histochemical profile of bag_1 fibers is very close to that of SO fibers, whereas the profile of chain fibers resembles that of FOG fibers (cf. Barker 1974). The matching of characteristics between intra- and extrafusal muscle fibers might possibly account for the predominance of type S among dynamic β units and of type FR among static β units.

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