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DIVISION OF MOTOR UNITS IN MEDIAL GASTROCNEMIUS MUSCLE OF THE RAT IN THE LIGHT OF VARIABILITY OF THEIR PRINCIPAL PROPERTIES

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Abstract. Ninety-seven motor units of medial gastrocnemius muscle of the rat were examined. Among the examined motor units, fast (F) and slow (S) units were distinguished on the base of the presence or absence of sag reflex in unfused tetanus, induced by stimulation at 40 Hz. The fatigue test, in turn, permitted to distinguish fast fatigable (FF) and fast resistant (FR) units. Fatigue index was calculated using two techniques, the results of which differed significantly from each other. The following basic features of motor units were examined: contraction time, half-relaxation time and twitch force. A more detailed analysis of all characteristics of the units disclosed that their classification into fast and slow units on the base of the sag test alone was unjustified. A more appropriate classification resulted when multiple properties of the units were considered. The distinguished types of the units differed significantly from each other in the examined properties. On the other hand, a significant individual variability in the properties was also shown to exist within each type of the units. Various characteristics of the motor units showed correlation with each other in the whole population of motor units and/or their individual types.

INTRODUCTION

Classification of motor units has already been made by several authors. The motor unit division suggested by Burke et al. (5), on the base of functional properties has been generally accepted. Their division takes into account the sag reflex in unfused tetanus of fast motor units and the results of the fatigue test. The authors have failed to employ other properties, as twitch force, tetanus tension, contraction time for the classification of motor units. Other authors also investigated these motor unit properties, but they have not considered their suitability as a basis of classifiction of motor units (20, 27).

In our earlier papers (Celichowski, in preparation; 12 - 14), we have presented some characteristics only of the medial gastrocnemius muscle of the rat, dividing its units mainly as described by Burke et al. (5). In the present work, apart from using the earlier techniques for more accurate classification of motor unit types, we have analyzed the sag reflex at various frequencies of stimulation and we have employed two techniques for calculating the fatique index. We have aimed at providing a more accurate description of motor unit types in the examined muscle and determining of how suitable are the examined properties for distinguishing the types of the units.

MATERIAL AND METHODS

Ninety-seven motor units of medial gastrocnemius muscle were examined in 54 rats of Wistar strain, weighting on the average 305 ± 52 g. A portion of the presented material was analyzed also in earlier publications (Celichowski in preparation; 12, 13). The earlier papers included the description of pentobarbital anesthesia and details of the surgery. In our experiments, the twitch force of muscle fiber was registered using an inductive transducer in isometric conditions, at passive stretching of the muscle (using, approximately, 10 g force), permitting usually to measure peak values of twitch force of the motor units. EMG records were obtained using a thin bipolar electrode inserted into the muscle (14).

In order to obtain the twitch of muscle fibers forming an individual motor unit, all ventral roots of spinal nerves in the lumbar region were transsected as well as all branches of sciatic nerve except the single branch supplying the medial gastrocnemius muscle. The ventral root of L5 was divided into bundles as fine as possible and, then, the latter were stimulated during the experiments.

Twitch force records were thought to reflect the twitch of a single motor unit if, at varying voltage of individual stimuli, they exhibited responses of all or none type. In this way, both twitch force and action potential records were evaluated. Stimulation of the motor units was effected using electric rectangular stimuli of 0.1 ms duration and up to 0.5 V amplitude. For stimulation we used bipolar silver electrode.

The motor units were subjected to the following tests: (1) recording a single twitch resulting from individual stimulation, (2) recording an unfused tetanus resulting from stimulation with a sequence of stimuli of the frequency of 20 Hz and, then, 40 Hz. Duration of each stimulating sequence was 500 ms. In the course of unfused tetanus, the presence or absence of the sag reflex was observed, (3) after 3 min pause a fatique test was performed, using unit stimulation with a series of stimuli, each of 40 Hz in frequency and lasting for 330 ms, repeated every 1 s for a total of 4 min. In the above procedure, the unit function was recorded using loop oscillograph (recording the tetanus course) and photographing oscilloscope sweeps of individual twitches as well as EMG sweeps.

For each motor unit, contraction time as well as half-relaxation time and twitch force were determined in individual twitch records. Contraction time was measured from the beginning of mechanical activity of the motor unit to the moment when force record showed the highest value. Half-relaxation time was measured from the latter moment to the moment when the recorded force decreased to half of its highest value. Twitch force was measured from the isoelectric level to the greatest deflection of the record.

In all fast motor units, secondary rise, i.e. an increase of tetanic tension during the first tens of tetani was noted. Due to the secondary rise, the resistance to fatigue of fast units was estimated using two techniques of fatigue index calculations, similarly as proposed earlier by Kernell et al. (18). The first technique of calculation involved dividing the value of tetanic tension noted 2 min after secondary rise had reached maximum by the value of tetanic tension recorded at the maximum of the secondary rise (Fig. 1 — A1 : A2). Fatique index calculated according to the technique was termed the fatique index A (18). The other technique, yielding the fatigue index B involved dividing the value of tetanic tension recorded 2 min after fatigue test start by the value of tetanic tension of the second tetanus (Fig. 1 — B1 : B2). In contrast to Kernell et al. (18) who employed tetanic tension of the first tetanus for calculating the fatigue index B, in our studies we employed tetanic tension of the second tetanus (and in some cases of the third tetanus) since, beginning at the second (third) tetanus, their tension started to increase: the tension of the first tetanus used to have a much higher value than the tension of the second one (Fig. 1). This phenomen as well as the secondary rise, were described in detail earlier (Celichowski, in preparation). The fatigue index for the slow units was calculated using only one technique, since such units showed no secondary rise. The units exhibited the highest tension at the first tetanus. Thus, in slow motor units the fatigue index was calculated as the ratio of tetanic tension noted 2 min

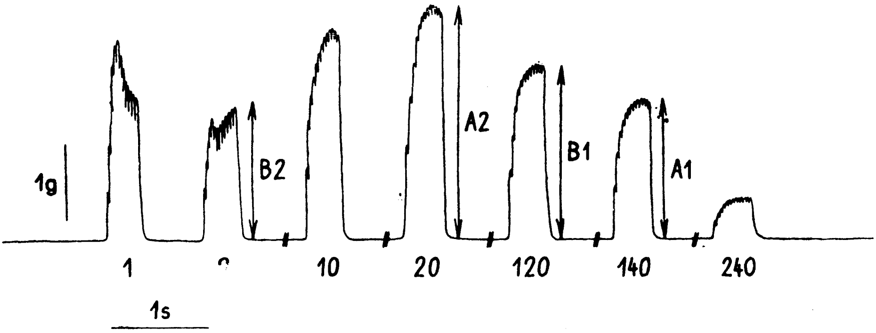


Fig. 1. Fragments of tetani records in FR type motor unit in the course of fatigue test. Number under the record indicate time of recording (in seconds from the beginning of the test). B2, tension of the second tetanus; A2, tension recorded at the end of secondary rise (the highest tetanic tension); B1, tension of tetanus recorded 2 min after fatigue test start; A1, tetanic tension recorded 2 min after the end of secondary rise.

after fatigue test start to the tension of the first tetanus (10). Comparing the resistance to fatigue between slow and fast motor units, the slow motor unit fatigue index values were compared with values of fatigue indices A and B for fast motor units.

In this study we calculated mean values of investigated characteristics, their standard deviations and correlations coefficients. The significance of differences between the means was tested using *t*-Student test.

RESULTS

Sag test

In the majority of 70 fast motor units, the stimulation at 20 Hz frequency induced sequential, nonsummative individual responses (Fig 2*A*). In 7 of the units (1 FF and 6 FR) showing a relatively long contraction time (17 - 20 ms), the stimulation at 20 Hz frequency resulted in weakly fused tetanus exhibiting a slight sag (Fig. 2*C*). On the other hand, stimulation at 40 Hz resulted in 68 out of 70 examined fast units in unfused tetanus, mostly with a well marked sag (Fig. 2 *B* and *D*). The remaining two fast units (both of FF type) developed at such stimulation an unfused tetanus with no sag. They were thought to represent fast units due to short contraction times (14 and 17 ms) and short half-relaxation times (10 and 11 ms, respectively), significant potentiation of tetanic tension at the beginning of fatigue test and high fatigability (fatigue index A of the units amounted to 0.42 and 0.41, respectively).

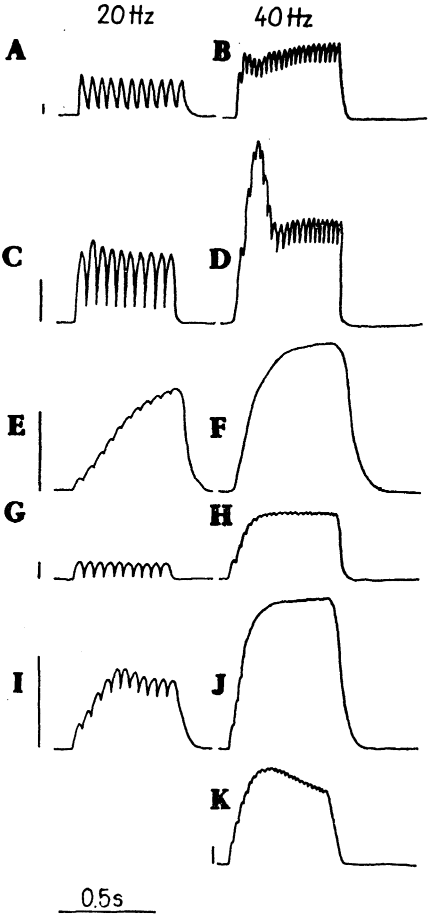


Fig. 2. Records of sag test in fast motor units of FF type (A, B), FR type (C, D) and in 4 slow units (E - K) at 20 Hz stimulation (left column) and 40 Hz stimulation (right column). Twitch force calibration — 1 g in all parts of the Figure.

The slowly contracting motor units at 20 Hz stimulation usually developed unfused tetanus with no sag reflex (Fig. 2*E*). However, 4 units out of 27 investigated slow motor units with a relatively short contraction time (18 - 22 ms) developed no tetanus but, instead, sequential, non-summative individual responses (Fig. 2*G*), similarly to the majority of fast motor units. In other 6 slow motor units, also of a relatively short contraction time (19 - 25 ms), the sag reflex was present in an unfused tetanus (Fig. 2*I*). On the other hand, stimulation at 40 Hz induced a fused or almost fused tetanus in 26 out of 27 slow units with no sag reflex (Fig. 2*F*, *H* and *J*). The remaining one slow motor unit developed, at such stimulation, an unfused tetanus with sag reflex (Fig. 2*K*). However, the tetanus course was somewhat different in this case than in the majority of fast units since the peak of tetanic tension was reached later than during tetani of fast motor units. The course of the fatigue test of this motor unit was typical for slow units. Contraction time of the unit was 22 ms and half-relaxation time was 20 ms. For these reasons the motor unit was included in slow units.

Fatigue index

Resistance of the motor units to fatigue was examined using fatigue test. After measuring tetanic tension of individual tetani in the fatigue test, values of fatigue indices A and B were calculated for each fast motor unit (see Methods). Histograms of fatigue index A values ranged from 0.0 to 1.0 (Fig. 3*A*). For fast motor units they showed bimodal distribution with a gap in the distribution around the index value 0.5. Fast units (46 of them) showing fatigue index values below 0.5 were taken to represent fast and rapidly fatigable motor units of FF type while fast units showing values of fatigue index above 0.5 (24 units) were taken to represent fast units resistant to fatigue (FR type). No intermediate FI type units were distinguished. Mean values of fatigue

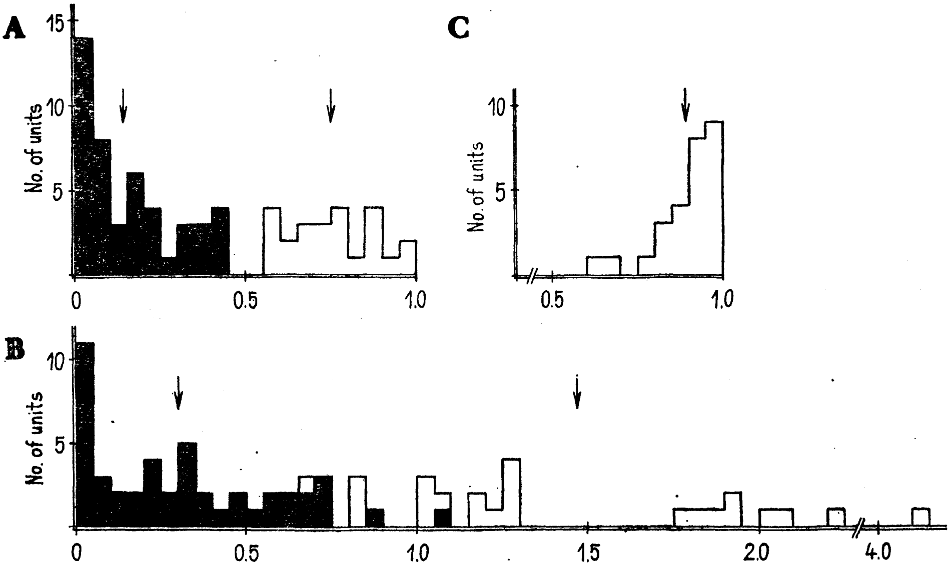


Fig. 3. Values of fatigue index A (part A of the graph) and fatigue index B (part B of the Figure) of fast motor units and values of fatigue index of slow units (part C). In the graph, FF units were marked in dark, FR and S units by light boxes. Arrows indicate mean values of fatigue indices for individual types of units.

TABLE I

Mean values of studied features in motor units of various types, their standard deviation and variability range. CT, contraction time; HRT, half-relaxation time; TwF, twitch force; FIA, fatigue index A; FIB, fatigue index B. The same abbreviations were used in other Tables and Figures

Motor unit type		CT (ms)	HRT (ms)	TwF (g)	FIA	FIB
FF	$n = 46$	15.5± 1.7	11.4± 2.0	2.27±1.48	0.14±0.13	0.30±0.27
		13.0—20.0	8.5∓17.0	0.20∓5.40	0.00—0.42	0.00—1.07
FR	$n = 24$	16.4± 1.8	13.0± 2.3	1.22±0.78	0.75±0.13	1.47±0.70
		14.5—20.0	9.5—19.5	0.50—4.30	0.57—1.00	0.65—4.13
S	$n = 27$	27.6± 6.2	28.5± 9.8	0.54±0.43	0.89±0.09	—
		18.0—40.0	15.0—32.0	0.11—1.75	0.63—1.00	—
F	$n = 70$	15.8± 1.8	11.9± 2.2	1.91±1.37	0.35±0.31	0.70±0.72
		13.0—20.0	8.5—19.5	0.20—5.40	0.00—1.00	0.00—4.13
S	$n = 97$	19.2± 6.4	16.8± 9.4	1.53±1.34	0.50±0.36	—
F		13.0—40.0	8.5—52.0	0.11—5.40	0.00—1.00	—

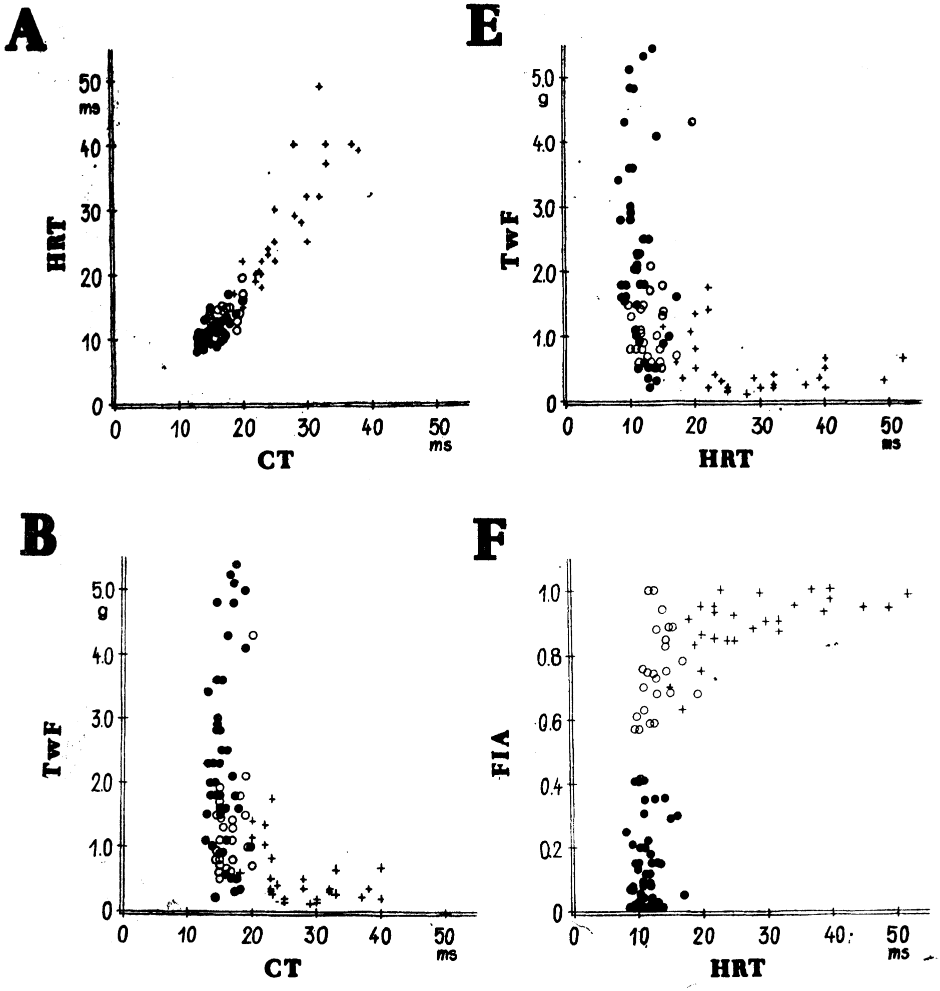
index A are given in Table I and are 0.14 ± 0.13 for FF units and 0.75 ± 0.13 for FR units.

For each fast motor unit, values of fatigue index B were higher than corresponding values of fatigue index A and ranged from 0.0 to 4.13 (Fig. 3B). Some FF units constituted an exception, showing fatigue index equal 0.00 whichever technique was applied for calculating the index (i.e. they showed no tetanic tension after 2 min of fatigue test). Comparison of part A with part B in Fig. 3 shows that values of fatigue index B are scattered wider than values of fatigue index A. Values of fatigue index B for marginal FF and FR units overlapped. Mean value for fatigue index B for FF units was 0.30 ± 0.27 (range 0.00 to 1.07). Twelve FF units which showed fatigue index B higher than 0.5, exhibited relatively high values of fatigue index A (mean 0.30, range: 0.12 to 0.42). Values of fatigue indices A and B correlated with each other for FF type units ($r = 0.877$, $p = 0.01$). The greatest difference between values of fatigue index A on one hand and B on the other in a single unit of FF type was 0.66 (range: 0.41 to 1.07).

Values of fatigue index B for FR type motor units were scattered more widely than in the case of FF units. In the group of FR motor units, values of the two fatigue indices failed to correlate with each other. In a majority of FR type units two minutes of stimulation are followed by tetanic tension higher than that noted at the second tetanus. Therefore, mean value for fatigue index B for FR units was greater than 1.0 and amounted to 1.47 ± 0.70 (range: 0.65 to 4.13). Both in FF and FR units, the difference between values of fatigue indices A and B was highly significant ($p < 0.01$).

Fatigue index for the slow units was calculated by one technique only (see Methods). It amounted to 0.89 ± 0.09 and in a majority of cases was lower than 1.0 (Fig. 3*C*). This reflects a slight tetanic tension decrease during first seconds of the fatigue test with an absence of increase in tetanic tension in the latter part of the fatigue test or with an increase which failed to compensate the preceding decrease.

In few slow motor units only a gradual, even if relatively slow, decrease in tetanic tension was observed. The two most fatigable slow units (fatigue indices 0.63 and 0.65) exhibited also the shortest contraction time (18 and 20 ms, respectively; Fig. 4).



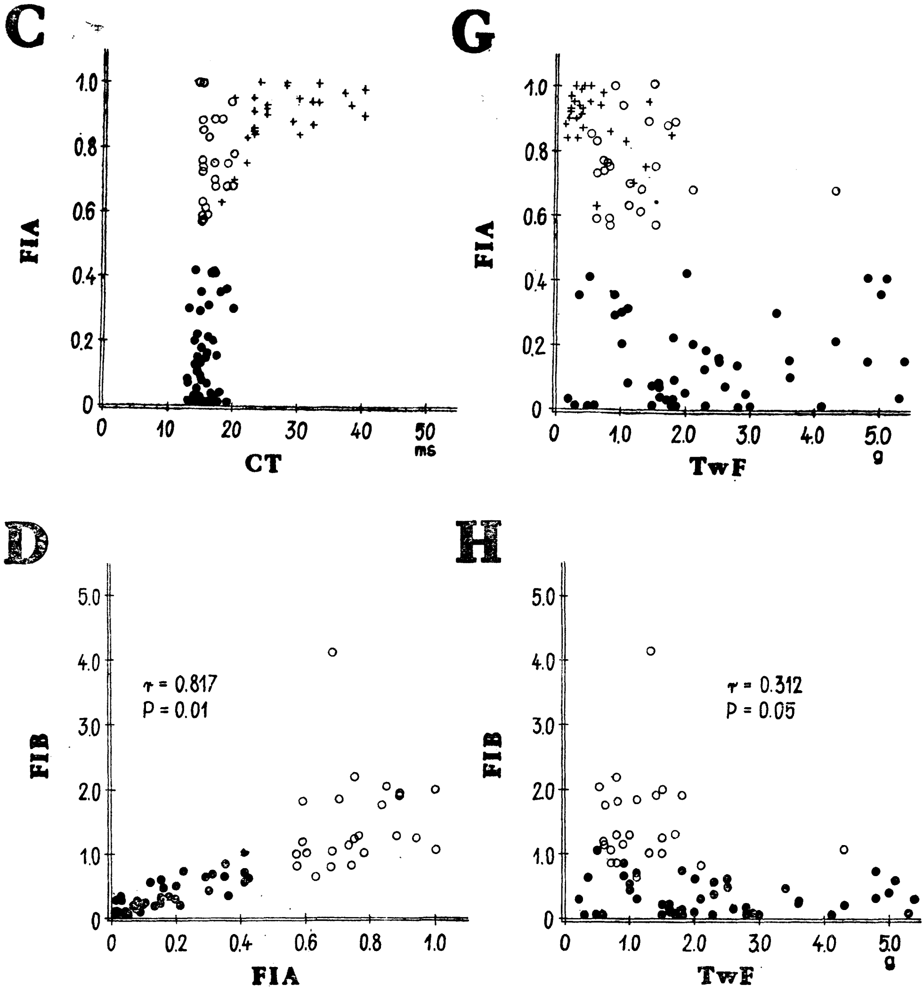


Fig. 4. Distribution of values in studied properties of motor units (for cases when significant correlation was found between the two properties — see Table III). FF units were marked by dark circles, FR units by open circles, S units by crosses. In part D and H of the Figure slow units were not marked. Correlation coefficients, calculated for fast units alone are also given in parts D and H. In the remaining parts of the Figure fatigue index of slow units was presented together with values of fatigue index A for fast units.

Comparison of other properties between motor units of various types

Apart from fatigue indices A and B, Table I presents also mean values of contraction time, half-relaxation time and tetanic tension for motor units of various types. The motor units of FF type exhibited the shortest contraction time and half-relaxation time (15.5 ± 1.7 and 11.4 ± 2.0 ms, respectively) and the highest twitch force (2.27 ± 1.48 g). Units of FR type showed, on the average, longer contraction time, longer half-relaxation time (16.4 ± 1.6 and 13.0 ± 2.3 ms, respectively) as well as lower twitch force (1.22 ± 0.78 g). Units of S type, in turn, manifested the longest contraction time and the longest half-relaxation time (means of 27.6 ± 6.2 and 28.5 ± 9.8 ms, respectively) and the lowest twitch force (0.54 ± 0.43 g). It should be mentioned that marginal values of contraction time, half-relaxation time and twitch force for fast units and for slow units overlapped (see Table I, Fig. 4). In the case of FF and FR type units the overlapping was also present and even more evident.

Estimation of differences in the mean values of contraction time, half-relaxation time, twitch force and fatigue indices A and B between individual types of motor units is presented in Table II. Comparison of the two types of fast motor units indicated that they differ from each other markedly in resistance to fatigue, half-relaxation time and twitch force while differences in contraction time proved less significant. When, in turn, the variables were compared between FF or FR units and S type units, all differences were found highly significant. Similar results were obtained when the whole group of fast units was compared with slow units. The only discrepancy involved the absence of significant difference in the mean value of fatigue index B between fast units and slow units.

TABLE II

Statistical significance of differences between mean values of features for various types of motor units

Feature	Comparison of motor unit types			
	FF—FR	FF—S	FR—S	F—S
CT	*	**	**	**
HRT	**	**	**	**
TwF	**	**	**	**
FIA	**	**	**	**
FIB	**	**	**	—

** $p < 0.01$; * $p < 0.05$; — difference not significant.

Correlations between properties of motor units in the studied population

In order to examine correlations between the studied properties of the motor units, correlation coefficients were calculated between feature values for the whole studied group of 97 motor units. Results of the calculations are presented in Table III. Similar correlations were also examined in individual three groups of various unit types. As evident in Table III, contraction times and half-relaxation times correlated strongly with each other. The properties correlated with each other also in each of the three types of motor units (r = 0.685, 0.634 and 0.841 for FF, FR and S type units, respectively, $p < 0.01$ in each case).

TABLE III

Correlation coefficients for studied features of motor units, calculated for the whole studied population

	CT	HRT	TwF	FIA
HRT	0.938**	—	—	—
TwF	—0.408**	—0.439**	—	—
FIA	0.632**	0.630**	—0.500**	—
FIB	0.164	0.192	—0.336**	0.696**

** $p < = 0.01$.

As evident also in Table III, contraction time strongly correlated with twitch force and the fatigue index A, while half-relaxation time correlated with twitch force and the fatigue index A. No correlation was noted between contraction time or half-relaxation time and fatigue index B. Twitch force was found to correlate with each of fatigue indices, A and B. The two fatigue indices correlated with each, other.

It should be added that within the slow motor unit group, correlations were noted between contraction time and fatigue index ($r = 0.517$, $p < 0.01$), between half-relaxation time and fatigue index ($r = 585$, $p < 0.01$) while weak, negative correlations were observed between twitch force on one hand and contraction time ($r = -0.463$, $p < 0.05$) or fatigue index ($r = -0.388$, $p < 0.05$) on the other.

Apart from the mentioned correlation above between fatigue index A and fatigue index B in the group of FF motor units, no other strong correlations were observed between the studied properties of fast units within their two types.

Relations between values of the studied properties, between which correlations were detected within the studied population of motor units, are presented also in Fig. 4.

DISCUSSION

Division of motor units into fast and slow ones, based on functional properties, was performed in various ways by different authors. Most of the authors used for the purpose the presence of sag reflex in an unfused tetanus of motor unit (4, 5, 7, 9, 18, 25), others employed contraction times, separating them arbitrarily into slow and fast ones (11, 17, 27). Kernell et al. (18) tried to distinguish fast and slow units on the ground of the so called force rise index. Each of the techniques showed certain deficiencies (18, 25, 27). The situation is made even more difficult due to the absence of sag reflex in some fast units and because the sag reflex is present in some slow units tetani induced by low frequency stimulation (3, 10, 17, 25, 27). It is also known that the ranges of contraction time of slow units (i.e. with no sag in unfused tetanus) and fast units may overlap each other in some muscles (6, 15, 21, 26). For these reasons, to separate from each other such atypical motor units of the posterior tibial muscle, McDonagh et al. (25) considered, apart from the sag reflex, also some other properties. However, the authors have not observed in their experiments the secondary rise.

In the presented experiments we have found three motor units in which the majority of properties (contraction time and half-relaxation time, twitch force, fatigue resistance or the course of fatigue test) indicated that the units have belonged to types distinct from those which would be pointed by the presence or absence of sag reflex in unfused tetanus. It should be stressed that the secondary rise, beginning from the second (third) tetanus in the course of fatigue test in all fast units (Celichowski, in preparation) is an evident property which can assist in the classification of motor units into slow and fast ones. The presented experiments have confirmed the usefulness of sag reflex for differentiating the units of medial gastrocnemius muscle in the rat, but it should be added that the final classification of the units should be verified by a set of properties.

The motor unit classifying system into fast and slow ones according to Burke et al. (5) has been based on the presence of sag reflex in the tetani of fast units and on the absence of such reflex in slow units, when the motor units are stimulated at a frequency reciprocal to 1.25 x contraction time for a given unit. In our experiments on rat units, the presence of sag reflex has been controlled in tetanic tension records obtained at stimulation frequencies of 20 Hz and 40 Hz. In a majority of fast units, 20 Hz stimulation has failed to induce tetanus. In the slow units, on the other hand, it usually has induced tetanus with no sag even if, in some units (6 out of 27 units) the sag has been present at such frequency of stimulation. According to our observations, 40 Hz stimulation allows better differentiation of motor units into fast and slow types. The stimulation has been found equally effective to the stimulation with frequencies reciprocal to 1.25 x contraction time, calculated separately for each individual unit (5). This is even more so, since the motor unit classification has to take into account also properties other than the sag reflex. It should be mentioned that contraction time of motor units in the rat is less variable than in the cat (2).

Fast motor units of different muscles exhibit extensive variability of resistance to fatigue (2, 3, 8, 20). In order to examine this property, several authors apply fatigue test, described by Burke et al. (5). The authors have introduced the fatigue index corresponding to the ratio of tetanic tension of the unit after 2 min of the test to tetanic tension of the first tetanus. Since Burke et al. (5) have induced in their experiments tetanic potentiation before performing the fatigue test itself, during the test they have observed only a decrease in the tension and fatigue index values have ranged between 0.0 and 1.0. The fatigue index introduced by Burke et al. (5) has been modified by Kernell et al. (18), who have observed an increase in tetanic tension (secondary rise) in the first part of the fatigue test and they have calculated the fatigue index as a ratio of tetanic tension recorded 2 min after the end of secondary rise to tetanic tension noted at the end of secondary rise. This way of calculating fatigue index (fatigue index A) has been used also in this study and it corresponds to the fatigue index of Burke et al. (5).

Values of fatigue index A differ from values of fatigue index B which has also been calculated. The difference results mainly from the potentiation of tetanic tension, which developes in the course of fatigue test. Due to the potentiation, values of fatigue index B are higher than corresponding values of fatigue index A (Fig. 1). The difference between the values of the two indices is greater in the FR unit group than in the FF unit group. It should be added that the two indices failed to correlate with each other in the FR unit group. This lack of correlation seems to result from potentiation of tetanic tension, which remains highly variable in individual FR type units. It should be recalled that after 2 min of the test tetanic tension of FR units used to be still markedly potentiated. Some authors have suggested ways of calculating fatigue index distinct from that given by Burke et al. (5): e.g. they have been basing calculations on the estimation of tetanic tension in all tetani or on integrating area under tetanus record line (10, 17, 18, 27). The different ways calculating the fatigue index have yielded similar results (10, 18). In the presented experiments, we have restricted ourselves to calculating the index in the two above described ways. Analyzing the results, marked differences have been noted between indices A and B in FR units (and, somewhat smaller differences, also in FF units). For that reason our results are divergent from those of Kernell et al. (18). In experiments of those authors, the values of the two fatigue indices have been similar. This seems to be due to other measurements (dependence of motor unit tension upon stimulation frequency) which the authors have performed on the studied motor units before performing the fatigue test. Possibly, the measurements have partially potentiated the tension of studied units and, thus, have decreased the difference between the values of the two fatigue indices.

In our studies we have based the classification of fast motor units (division of fast units into distinct functional types) on the values of fatigue index A. The values are not affected by the secondary rise, which is strongly variable by itself. The fatigue index A correlates better with other properties of the units than the fatigue index B. In the medial gastrocnemius muscle of the rat we have divided the fast units into two types only, i.e. into FF and FR units and we have not distinguished an intermediate type. Such division has reflected the bimodal distribution of the fatigue index A values, with threshold values around 0.5 (Fig. 3*A*). The proportion of fast motor units population which according to some authors is formed by FI type motor units, is very variable. The evidently intrmediate type of muscle fibers, which would clearly correspond to fast units of the type, is difficult to demonstrate also in histochemical studies (5, 11, 15, 23, 25, 27). Histochemical studies of the medial gastrocnemius muscle in the rat, performed by Schmalbruch and Kamieniecka (28), have demonstrated also a bimodal distribution of enzyme activities correlating with resistance to fatigue in type II fibers. Also other authors have accepted a division of fast motor units into two types only (16, 18, 19), as shown in our study.

In contrast to our results, in motor units of the tibial anterior muscle in the rat other authors, e.g. Kugelberg and Lindegren (22), and many authors in various units of cat muscle (1, 11, 24, 27) have detected a continuous distribution of fatigue index values even if clear accumulation of motor units has been observed at each end of the range.

The presented studies show that FF units, as compared to FR units, are stronger, have shorter contraction times and half-relaxation times. These relations have also been described earlier (5, 6, 11, 15, 26).

In contrast to Kanda et al. (16), who conducted studies on tetanic tension of FF and FR type motor units in the same muscle (also in the rat), our experiments have revealed a significant difference between the twitch force of FF units on one hand and FR units on the other. Our results confirm the observations of McDonagh et al. (26). The authors have found that the difference in twitch force between FF and FR units is greater than such difference between FR and S units.

Curves of interrelationships between the studied properties of motor units of medial gastocnemius muscle in the rat show, in multiple comparisons, the so called L-shape (Fig. 4*B*, *C* and *E* - *G*). Curves of a similar shape have also been noted in studies on cat muscle units (3, 5). Such distribution of results reflects, in both animal species, a significant scatter of contraction time and half-relaxation time values in slow units, a high scatter of resistance to fatigue and of twitch force in fast units. Both are paralleled by relatively similar values of contraction time and half-relaxation time in fast motor units and relatively similar twitch force and resistance to fatigue in slow motor units.

Within slow motor units, the ones with the shortest contraction time used to show also the shortest half-relaxation time, relatively high twitch force and the lowest values of fatigue index. Thus, in respect to the above mentioned properties the motor units resemble FR units, but differ from fast units by the absence of secondary rise in the course of fatigue test and, with a single exception in our experiments, by the absence of sag in tetanus induced by 40 Hz stimulation. The relatively low fatigue index values in two of the units originate from progressing fatigue and, in the other, stem from a marked decrease in tetanic tension at the beginning of fatigue test. In subsequent tetani, up to the end of the fatigue test, tetanic tension has been constant in the motor units.

The presented results, which take into account some principal properties of motor units, point to a very marked variability in each of the properties not only between different types of the motor units but also within each type. Change in the value of one property does not necessarily lead to changes in the remaining properties. The variability affects also the properties which are accepted as basic for the classification of the motor units (sag reflex, contraction time, resistance to fatigue). Therefore, type determination for any unit should take into account a relatively high number of properties of the motor unit.

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