

## INTERSPECIES DIFFERENCES OF MOTOR UNITS PROPERTIES IN THE MEDIAL GASTROCNEMIUS MUSCLE OF CAT AND RAT

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### INTRODUCTION

Motor behaviour, locomotor activity and the patterns of overground walking of rats and cats show significant diversities (15, 16). It obviously suggests considerable differences in proportions, morphological and mechanical properties of motor units as well as in the course of generated contractions of respective muscles. Central mechanisms controlling locomotion and voluntary movements in these two species are also different (18) and discharge firing rates of motoneurons in decerebrate or freely moving animals have been found significantly higher for rats than for cats in studied muscles of hind limbs (20, 21, 33). Main contractile properties of isolated motor units have been commonly investigated electrophysiologically and several issues on the regulation of force and motor control have been solved for single and tetanic contractions of motor units in various muscles of rat and cat. Surprisingly, the comparison of results obtained in numerous experiments performed for past decades is often not easy, since in various laboratories different methods have been introduced for these species. On the other hand, some discrepancies between respective features of motor units of rats and cats have appeared difficult to compare since different muscles have been used for evaluation. Moreover, in many cases the problems undertaken by various research groups have only fragmentarily overlapped, even for the same species and the same muscle.

Cats and rats have been commonly used as the model animals in the majority of functional studies on single, isolated motor units, and the medial gastrocnemius muscle has been most often explored (3, 5, 22, 23, 26, 28). Our previous work, concerning mechanisms of the regulation of muscle force generated in unfused tetani, has also been performed on the medial gastrocnemius muscle, in both rats and cats (6, 10). However, no systemic comparison of motor units' properties between these species has been made so far. Therefore, the purpose of the present study in the cat and rat was to investigate (with the same methods and under comparable conditions) motor unit properties of the medial gastrocnemius muscle. We have addressed three main questions related to this subject. The first question was whether rat and cat are

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different with respect to the composition and proportions of various types of motor units in this muscle. The second question was which mechanical properties of motor units best reflect interspecies differences. The third question was how these properties influence mechanisms of the regulation of muscle force during unfused tetani in rats and cats. Possible functional implications of established differences for rat and cat behaviour were later discussed.

## METHODS

### *Preparation*

Experiments were performed on deeply anaesthetized animals: four adult female cats (weighing 3.0–3.15 kg) and four adult Wistar female rats (weighing 250–340 g). All procedures followed the European Union guidelines of animal care as well as principles of the Polish Law on The Protection of Animals. Cats were initially anesthetized with ketamine hydrochloride, (Calypsol, 30–40 mg/kg, i.m.) and subsequently with  $\alpha$ -chloralose (in several doses, supplemented as required, up to a total dose of 50–60 mg/kg, i.v.). Rats were anesthetized with sodium pentobarbital (60 mg/kg, i.p., supplemented as required). Adequacy of the anaesthesia was verified in cats by the lack of withdrawal and corneal reflexes and by the diameter of pupils, heart rate and arterial blood pressure. Additional doses of anaesthetic were given when pupils dilated or the blood pressure rose. The blood pressure was continuously kept between 90 and 130 mmHg. In rats, withdrawal reflexes and respiratory rate (90–120/min) were monitored. Core temperature of all animals was maintained by automatic heating system at  $37 \pm 1$  °C. At the end of experiments animals were killed by overdose of pentobarbital sodium.

The medial gastrocnemius muscle was tested. In both species, the medial head of the gastrocnemius muscle of the hind limb was exposed and carefully isolated from surrounding tissues, while blood vessels to this muscle were left intact. The Achilles tendon was dissected free and connected to the force transducer. All the collateral branches of the sciatic nerve trunk were permanently severed except the one innervating the muscle investigated. The laminectomies were performed over the lumbar and sacral segments of the spinal cord, dura mater over L5–S1 segments was cut and retracted, and right dorsal and ventral roots were cut as proximally as possible to the spinal cord. Splitting L4–L5 ventral roots (in rats) or L7–S1 ventral roots (in cats) into the possibly thinnest filaments enabled us to functionally isolate single motor units.

Cats were immobilized with steel clamps at the thoracic and lumbar vertebrae, the hip and the tibia of the right hind limb, and the foot were attached to the steel rod. Skin flaps were pulled up around the back of leg to form the pool, filled with paraffin oil. Rats were immobilized with rigid frame; the tested hind limb was clamped with the knee at the angle of about 130° and inserted inside small chamber filled with mineral oil. The L1 and S1 vertebrae were also hang up by steel clamps. The operated hind limb and the exposed areas of the spinal cord were covered with paraffin oil; its temperature was automatically kept at  $37 \pm 1$  °C.

### *Stimulation and recording*

The Achilles tendon was attached to the force transducer by a low-compliance, small diameter line. To obtain the highest contractile force for individual motor units the muscle was stretched up to a passive tension of 400 mN (10) or 100 mN (7), for cats and rats, respectively.

Filaments of ventral roots were stimulated using a bipolar silver wire electrode, with suprathreshold, rectangular pulses of 0.1 ms duration and variable amplitudes (up to 1.5 V) produced by the dual channel square pulse stimulator (Grass Instrument Company, model S88). Motor unit action potentials from the medial gastrocnemius were recorded with a silver bipolar electrode inserted into the muscle, perpendicular to his long axis. Signals were amplified with the low-noise multi-channel preamplifier (WPI, model ISO-DAM8-A, with a high-pass filter at 0.1 Hz and a low-pass filter at 10 kHz). All isometric force measurements were made by the force transducer

(model FT-510, force sensitivity of 100  $\mu$ m per 100 mN). When the evoked contraction and electrical activity in the muscle were "all-or-none" type, the response was accepted as indicative of a single motor unit (19, 23).

Force output and electromyogram were displayed on an oscilloscope screen, and recorded with analog-to-digital 12-bit converter (RTI-800 Utilities – the sampling frequency 1 kHz for force records and 10 kHz for action potentials), interfaced with a computer with appropriate software.

#### *Experimental protocol*

A specially designed computer program controlled activation of each isolated motor unit. The following stimulating protocol was applied for the cat: 1) five single pulses at 1 Hz (twitch forces and action potentials were averaged); 2) three trains of pulses at 15, 20 and 25 Hz stimulation frequency, during 900 ms (unfused tetani were evoked); 3) one train of pulses at 100 Hz during 300 ms of stimulation (a fused tetanus was evoked); 4) five single pulses at 1 Hz; 5) the fatigue test (14 impulses at 40 Hz repeated every second within 3 min). In rats, motor units were activated using the following protocol of stimulation: 1) five single pulses at 1 Hz (twitch forces and action potentials were averaged); 2) three trains of pulses at 30, 40 and 60 Hz stimulation frequency during 500 ms (unfused tetani were evoked); 3) one train of pulses at 150 Hz during 300 ms of stimulation (a fused tetanus was evoked); 4) five single pulses at 1 Hz; 5) the fatigue test (14 impulses at 40 Hz repeated every second within 3 min). In both protocols, individual stimulations were separated by 10-seconds intervals. Due to longer twitches observed in the cat, duration of unfused tetani applied to cat and rat was differentiated (900 ms vs. 500 ms, respectively) in order to obtain similar numbers of pulses in each record, for reliable comparisons of tetanic profiles.

#### *Data analysis*

For each averaged twitch record, the force (TwF, from the baseline to the peak), the contraction time (CT, from the beginning of mechanical activity to the peak force) and the half-relaxation time (HRT, time between the peak force and the half of this maximum value) were measured. For each fused tetanus record, the maximum tetanic force (TetF) was measured. The ratio of maximal forces of a single twitch and the fused tetanus were analysed as a twitch-to-tetanus ratio (Tw/Tet).

Extent of the fusion of the tetanus was measured as the "fusion index" (FuI) – ratio of the amplitude of the maximal relaxation before the successive contraction within tetanus, to the amplitude of this contraction (1, 8). FuI was calculated for the last contraction within each tetanus and varied from 0.0 (for sub-fused twitches, at lower frequency of stimulation), up to 1.0 (for the maximal, fused tetani). Differences in the profiles of unfused tetani of motor units were analyzed from records at comparable degrees of fusion, usually at 15-20 Hz for the cat and 40 Hz for the rat (Fig. 4).

Fatigue index (FI) was measured as a ratio of the contractile force generated two minutes after the most potentiated contraction at the beginning of the fatigue test, to the highest initial force (19, 25).

Motor units were divided on the basis of a sag effect (visible only in unfused tetani of fast motor units) and the values of the fatigue index (3). They fell into following categories: fast fatigable motor units (FF), with sag and the fatigue index under 0.5; fast resistant units (FR), with sag and the fatigue index above 0.5, and slow units (S), without sag and the fatigue index close to 1.0.

Student's *t*-test was used for statistical comparison of data obtained from two species.

## RESULTS

The total sample analyzed in this study consisted of 79 and 85 motor units, for the cat and rat medial gastrocnemius muscle, respectively. In the cat, the sample was divided into 54 FF, 14 FR, and 11 S motor units. In the rat, motor units were classified as follows: 31 of FF type, 44 of FR type, 10 of S type. Differences in composition of the studied muscle are shown as percentage in Figure 1. In the cat muscle fast

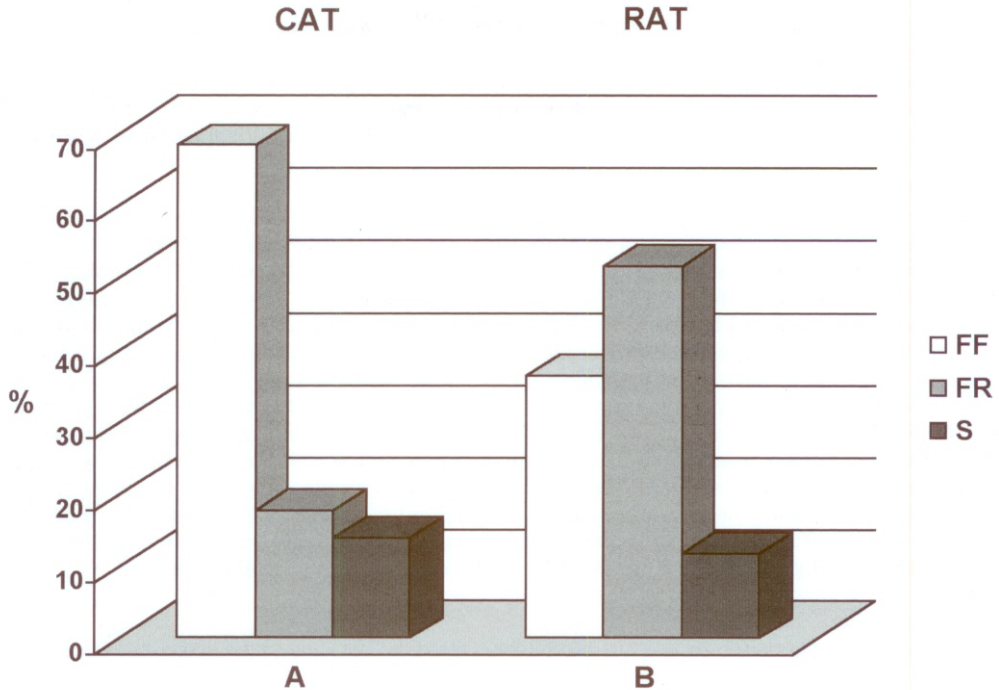


Fig. 1. - Motor unit proportions in the cat (A) and rat (B) medial gastrocnemius muscle. FF, fast fatigable (white bars), FR, fast resistant to fatigue (grey bars), S, slow motor units (black bars).

fatigable motor units predominated, and proportions of particular types were 68, 18 and 14%, for FF, FR and S units, respectively. In rats, the majority of motor units appeared to be fast resistant and proportions of FF, FR and S motor units amounted to 36, 52 and 12%, respectively. In both species, the division of motor units into fast and slow based on a sag phenomenon corresponded to differences in twitch contraction times of individual units. For cats, 11 units classified as slow had twitch contraction times  $> 44$  ms, while in 68 units classified as fast contraction times were  $\leq 44$  ms (Fig. 2A). For rats, in 10 slow units, with small variability with respect to twitch force and fatigability, twitch contraction times exceeded 20 ms, whereas in 75 fast units, showing great variability of fatigue resistance, contraction times were below 20 ms (Fig. 2B).

Mean values and standard deviations of the main contractile properties of all motor units of two studied species are compared in Table 1. In the cat, both slow and fast motor units had more than twice longer mean contraction and half-relaxation times than in rat motor units (Fig. 3). Differences were statistically significant ( $p < 0.01$ , Student's  $t$ -test). Moreover, even maximal values of CT obtained in the rat motor units did not overlap with minimal values of CT measured for respective types of feline motor units. Such overlapping was observed when ranges of HRT values were compared. Ratios CT/HRT were higher in the cat and amounted to the means 1.12 vs. 1.07 for FF units, 0.98 vs. 0.90 for FR units, 0.88 vs. 0.66 for S units, for the

cat and rat, respectively. For fast motor units, interspecies differences of CT/HRT ratios were not significant ( $p > 0.05$ , Student's  $t$ -test), indicating similar shapes of isometric twitches in both species. However, for slow motor units, mean values of this parameter significantly differed ( $p < 0.01$ , Student's  $t$ -test), confirming the relatively steeper initial phase and relatively longer relaxation phase that could be observed for majority of twitch records in the rat, in comparison to cat medial gastrocnemius units (Fig. 3C and F).

Twitch forces and maximal tetanic forces were considerably higher in the cat, but not equal for each type of motor units. In fast motor units, mean values of either TwF or TetF were found to be 7-8 times higher in the cat. In S motor units, however, only two times difference between both species was noticed for mean TwF, while approximately 5 times difference for mean TetF. Variability between twitch forces of individual motor units was much more pronounced in the cat medial gastrocnemius, in comparison to the rat muscle. 177 times difference was observed between the strongest FF and the weakest S motor unit within the whole population investigated in the cat, while only 40 times difference was noticed in the rat muscle. Within particular motor unit types, 20, 60 and 10-times differences between the strongest and the weakest unit were revealed in the cat for FF, FR and S units, respectively. The same comparison among rat units revealed only 14-times difference between the weakest and the strongest motor unit within groups of FF and FR units, and only 3.5 times difference among S units.

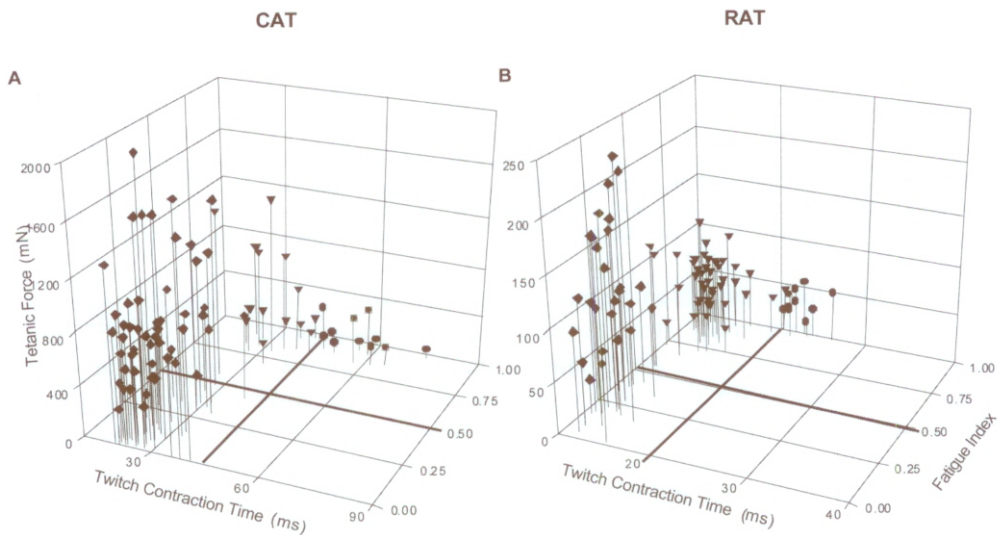


Fig. 2. - Distribution of motor units in the gastrocnemius muscle of the cat (A) and rat (B).

The three-dimensional diagram presenting interrelationships between the twitch contraction time, the maximal tetanic force, and the fatigue index. FF, fast fatigable (diamonds); FR, fast resistant to fatigue (triangles); S, slow motor units (circles). Thick solid lines in the diagrams indicate the border contraction times between slow and fast motor units – 44 ms for the cat (A), 20 ms for the rat (B) – as well as the fatigue index 0.5, separating FF and FR units.

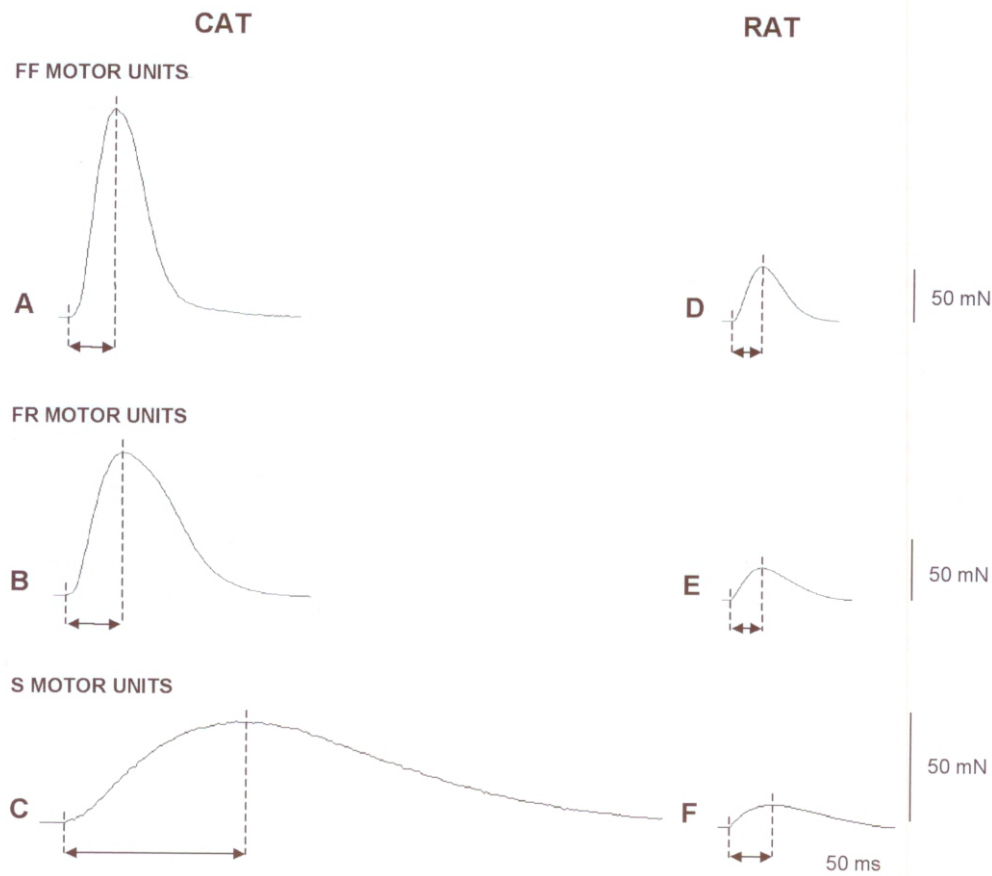


Fig. 3. - Comparison of the cat (A-C) and rat (D-E) isometric twitches, for three types of motor units, on the same time scale and with the same amplification for each motor unit type.

In each record, dotted vertical lines and arrows indicate contraction times – between the onset of the twitch and its maximal force. FF, fast fatigable, FR, fast resistant to fatigue, S, slow motor units.

On the other hand, twitch-to-tetanus ratios were similar in both species, especially for FF and FR motor units. Both in the cat and rat, mean Tw/Tet ratio for FF motor units was the highest, while for S units – the lowest. However, mean value of this parameter calculated for the cat S units was even twice lower than the respective value in the rat (0.07 vs. 0.13, Tab. 1). This observation correlated to the above-mentioned unequal differences between cat and rat S units with respect to twitch forces (2 times higher in the cat) and tetanic forces (5 times higher in the cat).

Table 1 also contains values of fatigue indices calculated for all groups investigated. The mean values were comprised in similar ranges for both species.

Figure 4 shows examples of unfused tetanic contractions of cat and rat motor units of all types distinguished in the study. The profile of tetanic contractions of slow motor units was similar in both species, and the sag effect was not visible (Fig. 4C and F). However, in FF and FR motor units considerable differences were noticed

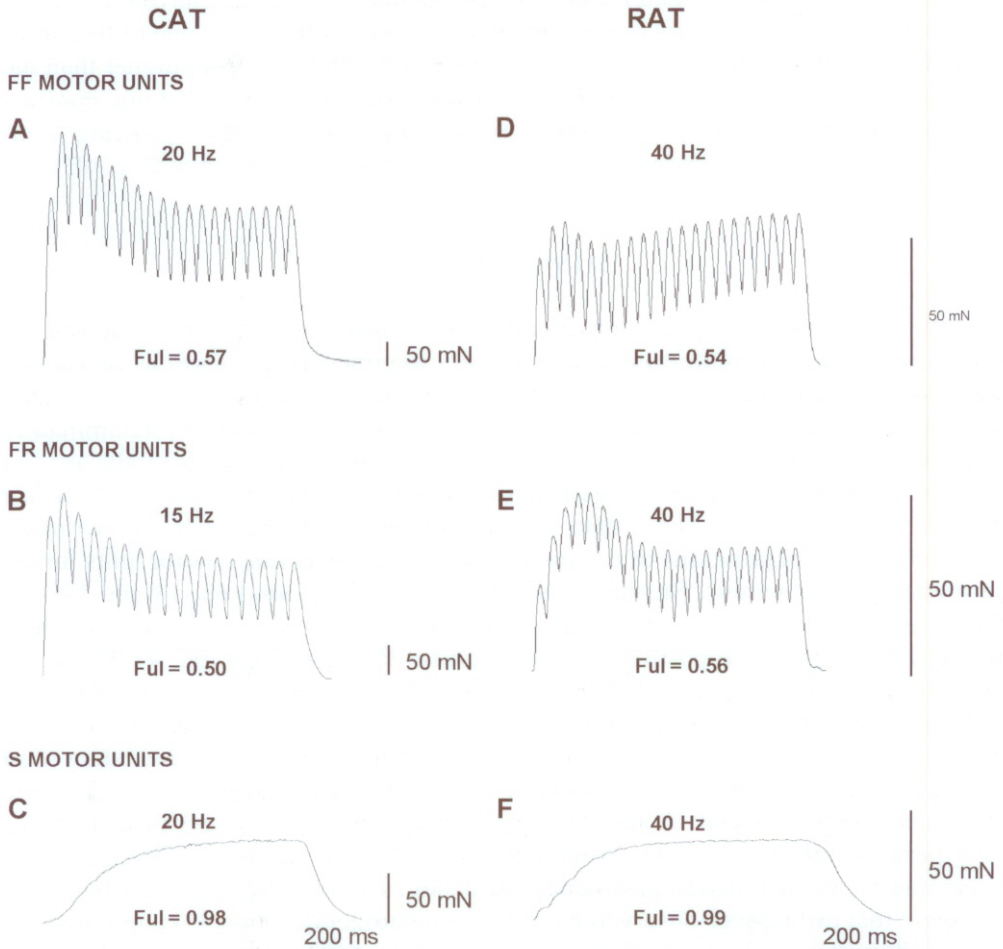


Fig. 4. - The presence of a sag effect during unfused tetanic contractions of three types of motor units of cat and rat.

A-C - feline motor units; D-F - rat motor units. The respective records taken from cat and rat muscle are compared at different stimulation frequencies, but at similar degree of fusion and with similar numbers of pulses in each contraction. Note differences between shapes of tetani for FF and FR motor units in the rat (D and E), that are invisible when compared records from feline motor units (A and B). FF, fast fatigable, FR, fast resistant to fatigue, S, slow motor units, Ful, fusion index.

between the species (Fig. 4A-B and D-E). For reasonable comparison, tetanic contractions with remarkable sag and similar fusion indices (between 0.5 and 0.7) were selected. Number of stimuli in these tetani was also similar and varied between 17 and 21. The above parameters were obtained in 15 or 20 Hz records for cat motor units and in 30 or 40 Hz records for rat motor units. In the cat, the profiles of unfused tetani for FF and FR units were similar, showing the initial increase in force to the maximum, then a "simple" sag effect - when force gradually decreased to gain a steady level (Fig. 4A-B) (5). Contrary to this, in the rat, two different shapes of sag

were distinguished. All unfused tetani of FF motor units were characterized by “complex” sag, with initial force increase to the peak, a short decrease for one to five stimuli, and then a second force increase that frequently reached the level higher than the initial peak (Fig. 4D). FR units in the rat muscle exhibited unfused tetanic contractions that firstly rose to maximum and decreased gradually thereafter, showing “simple sag”, that was longer and appeared later in comparison to FF units (Fig. 4E).

## DISCUSSION

In the present study we demonstrated several differences between cat and rat medial gastrocnemius motor units, with respect to either the proportions of various types contained in this muscle, contractile properties of single twitches or tetanic contractions. In cats, the medial gastrocnemius muscle is composed predominantly of fast fatigable motor units (68%), while in rats, the majority of motor units are fast resistant to fatigue (52%). The proportions of S units were similar – 14 and 12%, for cat and rat, respectively. These data are in agreement with previous studies made separately within populations of cat and rat medial gastrocnemius motor units. In the cat medial gastrocnemius, Stephens and Stuart (29) have found 68, 18 and 14% of FF, FR and S units, respectively. In the rat, Kanda and Hashizume (23) have demonstrated the following proportions of motor units: 35.4% of FF type, 47.9% of FR type, and 16.7% of S type, while Kadhiresan et al. (22) – 33, 44 and 23% of FF, FR and S units, respectively. Such differences in composition of the muscle may reflect different behaviour and activity patterns of animals investigated. Rats are rather used to walk, run and explore for most time of a day, while cats spend most of the time at rest and sleep (between 16 and 23 hours), being consecutively active usually for short periods only (4, 13, 24). From this point of view, the predominance of FF motor units in the cat medial gastrocnemius is not surprising. On the other hand, we are aware that differences observed in only one heterogenous muscle cannot be generalized. Similar comparison of other muscles of the hind limb is needed for more conclusive statements. No such comparisons have been made so far.

The considerable disproportions between the animals' weight and muscle mass are obviously the main reason of great differences in the force generated by all motor unit types and in the time course of their contractions. In our research, mean twitch forces were almost 7-8 times higher in feline motor units, and 5 times interspecies difference was found for slow ones. However, in the cat medial gastrocnemius, much higher variability range was found between motor unit twitch forces; 10-60 times difference was observed between the strongest and the weakest unit in cats, in comparison to 3,5-14 times in rats (see Results and Table 1). We suppose that these differences reflect various ranges of innervation ratios, as well as various fibre diameter and length of the muscles investigated in both animals. Previous studies have demonstrated that in the gastrocnemius muscle of the cat, the mean innervation ratio are comprised in the range of 450 to 750 (12), while the cross-sectional area (CSA) of muscle fibres from 2500 to 5290  $\mu^2$ , for S and FF motor units, respectively (2,

Table 1. - *Contractile properties of the three different types of motor units studied in rat and cat medial gastrocnemius muscle.*

| Motor unit type | n  | CT (ms)               | HRT (ms)                | TwF (mN)                  | TetF (mN)                   | Tw/Tet                     | FI                         |
|-----------------|----|-----------------------|-------------------------|---------------------------|-----------------------------|----------------------------|----------------------------|
| CAT             |    |                       |                         |                           |                             |                            |                            |
| FF              | 54 | 26.1 ± 5.3<br>(19-41) | 25.1 ± 9.8<br>(13-58)   | 231.8 ± 131.9<br>(27-531) | 841.8 ± 390.3<br>(251-1974) | 0.28 ± 0.14<br>(0.06-0.57) | 0.14 ± 0.14<br>(0.00-0.49) |
| FR              | 14 | 32.5 ± 6.5<br>(24-44) | 33.9 ± 9.2<br>(22-60)   | 83.8 ± 114.4<br>(6-360)   | 516.4 ± 404.4<br>(140-1320) | 0.14 ± 0.15<br>(0.03-0.6)  | 0.83 ± 0.10<br>(0.56-0.96) |
| S               | 11 | 56.6 ± 9.3<br>(44-75) | 68.5 ± 23.9<br>(42-116) | 9.1 ± 7.7<br>(3-31)       | 169.8 ± 119.8<br>(48-380)   | 0.07 ± 0.04<br>(0.03-0.15) | 0.91 ± 0.05<br>(0.84-1.00) |
| RAT             |    |                       |                         |                           |                             |                            |                            |
| FF              | 31 | 11.8 ± 1.6<br>(10-16) | 11.3 ± 3.1<br>(8-22)    | 33.6 ± 17.6<br>(6-81)     | 120.2 ± 52.1<br>(35-233)    | 0.28 ± 0.08<br>(0.11-0.4)  | 0.22 ± 0.11<br>(0.02-0.42) |
| FR              | 44 | 13.5 ± 2.2<br>(10-20) | 15.6 ± 4.6<br>(9-27)    | 12.1 ± 6.6<br>(2-27)      | 61.5 ± 26.3<br>(18-124)     | 0.19 ± 0.06<br>(0.05-0.31) | 0.85 ± 0.11<br>(0.55-1.00) |
| S               | 10 | 22.3 ± 1.7<br>(20-26) | 34.6 ± 6.4<br>(27-43)   | 4.5 ± 1.8<br>(2-7)        | 35.3 ± 13.3<br>(15-57)      | 0.13 ± 0.05<br>(0.08-0.3)  | 0.99 ± 0.02<br>(0.96-1.00) |

For each motor unit type mean values ± standard deviations and variability ranges are presented. CT, contraction time; HRT, half-relaxation time; TwF, twitch force; TetF, maximum tetanus force; Tw/Tet, ratio of twitch to tetanus forces, FI, fatigue index.

32). For the rat muscle, Kanda and Hashizume (23) have reported considerably lower values, using the glycogen depletion technique. The numbers of fibres contained in one motor unit have been comprised in the ranges: 44-77 for type S, 116-198 for type FR, and 221-356 for type FF units, while mean fibre areas have varied between 1983 and 3489  $\mu^2$  for S and FF units, respectively. Kadhiresan et al. (22) have achieved similar results in the rat; mean innervation ratios – 57, 185 and 333, while mean CSA – 1869, 2521 and 3176  $\mu^2$ , for S, FR and FF units, respectively. Such interspecies differences have also been found for motor units in other muscles. For example, mean innervation ratio for the tibialis anterior have amounted to 200 for the cat and to 118-132 only for the rat (14). The authors cited above have confirmed that innervation ratio and a total cross-sectional area are highly correlated with the tetanic force generated by these motor units. One must notice that interspecies differences in the length of muscle fibres and pennation angle may also influence the force generated, as well as twitch contraction times of motor units (31).

In our study, CT and HRT of single twitches in the cat muscle were approximately twice longer than respective values in the rat. However, both in the cat and rat, the division of the population into fast and slow motor units on the basis of twitch CT and on the basis of sag were fully equivalent (Fig. 2). It is worth noticing that CT ranges in both species did not overlap, what was not mirrored in the case of HRT, though differences between cat and rat muscles were statistically significant for both parameters of the twitch. For fast units, twitch contractions were comparable in shapes for both cat and rat motor units, and differences between mean twitch and tetanic forces were proportional for both parameters. The latter observation points on similar effectiveness of summation in FF and FR motor units. However, in the case of S units, differences in the profile of isometric twitch were found, with rela-

tively longer relaxation phase in the rat. Such different twitch profiles between two species have not been described previously, and can be related to the following observation. Namely, in both cat and rat, twitch-to-tetanus ratios were comprised in similar ranges for fast motor units, but they were approximately twice lower for S units in the cat (the mean 0.07), in comparison to the rat muscle (the mean 0.13). Additionally, only two times difference was noticed for mean twitch forces, while 5 times difference for tetanic forces measured in both animals. This indicates that in slow motor units, summation of twitches into tetanus is relatively more effective in the cat than in the rat medial gastrocnemius.

The described differences between CT and HRT are closely related to various modes of locomotion in cats and rats. Cats employ gait pattern in which phases of support on three limbs are alternated with phases of support on two limbs, homolateral and diagonal. The step cycle, either for fore or hind limbs is relatively long – comprised in the range 700–800 ms (15). In rats, the interlimb coordination is characterized by the support on diagonal limbs, with diagonal sequence and diagonal couplets, and the step cycle duration is only 300–400 ms (16). CT and HRT are also the major factors influencing the firing rate generated by motor units during their voluntary activity, what in turn determines the force output (12, 17). Fast motor units, of shorter twitch contraction times, are active at higher mean firing frequencies than slow units. Hennig and Lømo (20) have investigated discharge patterns in fast and slow motor units of extensor digitorum longus (EDL) and soleus (Sol) muscles, respectively. They have recorded firing rates ranging 48–91 Hz for EDL, while only 18–21 Hz for Sol motor units. Such dependence is likely to be applied to interspecies comparisons as well, so one may suppose that mean firing frequencies of the feline motor units would be lower in comparison to the motor units of the rat medial gastrocnemius. The recordings of a preferred firing range of motoneurons during voluntary contractions across vertebrate species, from turtle to human, have been in agreement with this suggestion and have indicated the decrease of a motoneuron discharge rate parallel to the increase of the motor unit contraction time (21).

Analysis of profiles of unfused tetani showed no interspecies differences between S motor units, i.e., without sag. On the other hand, “simple” and “complex” sag could be visible in the rat FF and FR motor units, respectively (see Results), while in the cat motor units, only “simple” sag effect was present in both types of fast motor units. Different course of unfused tetani in FF and FR motor units of the rat muscle has been revealed in our previous study (9). This property has been used to distinguish an FF from FR type on the basis of one unfused tetanus only (with  $FuI$  between 0.25 and 0.75). However, such differentiation of fast motor units into FF and FR types (at comparable fusion degree) appears to be impossible in the cat. Mechanisms underlying sag appearance are complex and not fully understood. Several metabolic processes may influence this phenomenon, such as transient changes in the phosphorylation state of the myosin light chains, kinetics of intracellular calcium fluxes, sensitivity of the contractile machinery to this ion, or efficacy of cross bridge formation (5, 11, 27, 30). Various forms of sag also suggest two dis-

crete processes responsible for its appearance in FF and FR units. The different profiles of unfused tetani with sag in both species investigated suggest that intrinsic properties of muscle fibres constituting particular types of respective motor units in the medial gastrocnemius vary between cat and rat, especially with respect to FF units, composed of type IIb fibres (compare Fig. 4A and D).

In conclusion, the interspecies differences investigated in the medial gastrocnemius motor units are best perceptible on: 1) proportions of the three types of motor units; 2) twitch and tetanic forces, and twitch contraction times – with respect to motor units of either type; 3) effectiveness of twitch summation into tetanus – with respect to S motor units; 4) the profiles of unfused tetani – with respect to FF and FR motor units. The presented differences reflect both the metabolic processes of muscle fibres and modes of locomotion or behavioral habits of both animal species. To extend the presented results and to connect them with more generalized analysis of movements of the limbs and variable locomotor patterns, similar interspecies comparisons of motor units in other muscles would be profitable.

#### SUMMARY

The purpose of the study was to analyze the interspecies differences of motor unit contractile properties in two most frequently studied mammals: cats and rats. A total sample of 166 motor units (79 in cats and 85 in rats) was investigated in the medial gastrocnemius muscle. Considerable differences were found in composition of the studied muscle. In cats, fast fatigable, fast resistant and slow units formed 68, 18 and 14% of the investigated population, whereas in rats 36, 52 and 12%, respectively. The contraction and relaxation times of motor units in the cat muscle were evidently longer than in the rat and the border values for fast/slow motor units division in these species were 44 and 20 ms, respectively. The mean values of twitch and tetanic forces appeared to be 7-8 times lower in rats, for fast, while 2-5 times for slow motor units. Also variability between the strongest and the weakest units within each type revealed differences 10-60 times in cats, whereas only 3.5-14 times in rats. The summation of twitches into tetanus for fast units was comparable in both species, but for S units was evidently more effective in the cat. In fast motor units' tetanic contractions evident interspecies differences concerned sag appearance and profiles of unfused tetani of FF and FR units. Differences in contractile properties described in the study may depend on the size, number and innervation ratio of motor units in the muscle of cat and rat, as well as their biochemical variability. Differences in composition of motor unit types and uneven mechanisms of force development may reflect biological adaptation to variable behaviour of cats and rats.

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