Muscle fiber type, number and size in the EDL and soleus of *Jaculus jaculus*

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ABSTRACT

The adaptation of the extensor digitorum longus (EDL) and soleus muscles of *Jaculus jaculus* to bipedal movement was examined. Fiber type, number and diameter in both muscles were analyzed and compared to mouse muscles. Total fiber number in *jaculus* muscles was higher than mouse. The EDL was dominated by FOG fibers, while the soleus was dominated by SO fibers. Fiber diameter appears to reflect the load placed on each filter type during locomotion. The relative ratios of the fiber types and fiber diameter in each muscle appears to be adapted to the bipedal mode of locomotion. The EDL being mostly fast and predominantly oxidative and glycolytic, while the soleus being purely slow with no glycolytic fibers.

INTRODUCTION

Adaptability may be regarded as a basic characteristic of life. The most adaptable tissues appear to be those which produce or are subjected to mechanical stresses. Unlike other tissues that respond to mechanical stimuli, muscle both creates and responds to mechanical actions.

The speed of muscle contraction and fatiguability and the type of motor unit that provides the force and power is determined by the type of movement that the muscle is habitually subjected to. Selective recruitment of these motor units provides varying levels of contraction to produce work both efficiently and economically (Goldspink 1981a; Mascarello *et al.* 1986).

Peter *et al.* (1972) classified striated muscle fibers into three major types according to their speed of contraction and metabolic properties. Slow-Twitch-Oxidative Fibers (SO) are slow contracting, easily recruited fibers with low excitation threshold and low force production. However, they are energetically quite efficient and fatigue resistant due to their aerobic energy supply which allows them to maintain sustained activity over long periods of time as for example during posture maintenance (Kovanen 1989). Fast-Twitch-Oxidative Fibers (FG) are fast contracting difficult to recruit fibers with high excitation threshold and high force production. They have poor thermodynamic efficiency for work production and fatigue rapidly because they rely on anaerobic oxidation. Fast-Twitch-Oxidative-Glycolytic Fibers (FOG) are essentially the same as FG fibers but with a mixed aerobic and anaerobic supply of

energy. Hence they are more fatigue resistant than FG fibers but are still adapted for high speed sustained type of activity.

Patterns of fiber distribution can be predicted within mammalian locomotive muscles according to their function. Deep muscles and deep portions of the fast extensor muscles are composed mainly of SO and FOG fibers and more peripheral portions have higher numbers of FG fibers. This pattern of distribution reflects an adaptation for the efficient use of energy (Armstrong & Laughlin 1985).

A general scheme of fiber recruitment at varying speeds of locomotion has been developed (Armstrong 1981; Roy *et al.* 1991): During quiet standing, muscular force is provided by the deep, slow twitch extensor muscles. When the animal walks SO and FOG fibers of the most superficial fast muscles are engaged. However, most of the power provided is still by the deep slow muscle. As the speed of running and galloping increases, more peripheral fibers in muscles and more peripheral muscles within muscle groups become involved, until during high speed galloping (or maximal vertical jumping) nearly all fibers within peripheral muscles maybe recruited to produce force and as more FG fibers are excited galloping increases. SO fibers of extensors continue to be active even at the highest speeds. This pattern of fiber recruitment indicates a specific functional role for each fiber type at different phases of the step cycle. For a muscle to be versatile it has to have several types of motor units with different intrinsic contractions speeds (Goldspink 1981a).

Facultatively bipedal animals like the jerboa *Jaculus jaculus*, use mainly their hindlimbs to move and to support their body weight. This type of movement is thought to have a major effect on the physiological and biochemical properties of the hindlimbs muscles. Williamson & Frederick (1977) studied three muscles of the lower leg of the ricochetal rodent (*Dipodomys merriami*) which is known to be highly specialized for hopping and a member of the family Dipodidae (to which the jerboa also belongs). Toe extension was observed to be of special importance during movement. The hindlegs of Dipodidae are at least 4 times longer than their front legs. Usually, the toes of the hind foot are three in number, and if 5 toes are found the lateral ones i.e. 1st and 5th, are rudimentary with three central digits actually supporting the foot. *Jaculus jaculus* is the smallest of the genus *Jaculus* having an average weight of 55 g. The animal moves along the ground with leaps that may reach 3 m in length. When foraging the jerboa walks on four limbs, but at all other times is bipedal (Clayton 1983). The mode of movement appears to affect muscle composition. Strength exercise like sprinting, weight lifting and throwing events, require high bursts of energy output. Studies performed on athletes and experimental animals subjected to these training programs, showed that although all fibers hypertrophied (increased in diameter) in response to training (Somineau *et al.* 1985; Hather *et al.* 1991; Morales-Lopez *et al.* 1991), the extent of this response varied among the different muscle fiber types. Type II fibers which are fast fibers exhibited larger cross-sectional area than fiber type I which are slow (Ryushi & Fukuanaga 1986; Jackson *et al.* 1990). In addition, the percentage of type II fibers tended to increase more than type I fibers (Staron *et al.* 1990; Jansson *et al.* 1990). On the other hand, distance running, marathon and cycling are types of endurance exercise requiring continuous oxidative energy. The oxidative capacity of the major fiber types, especially SO and FOG is improved in endurance training, hence more power output can be generated (Howald 1985; Mackova *et al.* 1986; Costill *et al.* 1987). Endurance training does not seem to influence the cross-sectional area of the muscle fiber. The increase of the

proportion of SO and FOG fibers is believed to be a result of a transformation process leading to the conversion of type IIB (FG) into type IIA (FOG) and type IIA into type I (SO) (Simoneau *et al.* 1985; Gouble & Marini 1987; Rube & Secher 1991).

Little is known about the effect of vertical jumping on hindlimb muscles. Experiments on rats with amputated forelimbs showed an increase in the total hindlimb weight compared to controls (Davids *et al.* 1964). Another study indicated a decrease in type I fibers and an increase in type II fibers in the rat soleus (Pousson *et al.* 1990). Where bipedal animal locomotion and hopping falls amongst these different types of 'exercise' is not clear. It might be expected that this highly specialized way of locomotion in the desert hopper *Jaculus jaculus* would affect the mechanical as well as the histochemical properties of the hindlimb muscles. The present study attempted to examine fiber type distribution and sizes in two hindlimb muscles of the *Jaculus jaculus* so as to obtain a better understanding of the adaptation of these muscles to bipedal locomotion.

MATERIALS AND METHODS

Adult specimens of the desert jerboa *Jaculus jaculus* were trapped during night at a site in the desert near Wafra (south of Kuwait city). They were sacrificed by ether overdose as soon as they were brought to the laboratory to minimize any effect of caging on muscle properties. For comparison purposes MF1 Albino mice were obtained from the animal house (Faculty of Science, Kuwait University). At least 5 males and 5 females of each species were used for each experiment. After sacrifice animals were weighed, sexed and the extensor digitorum longus (EDL) and soleus muscles of the right limb were dissected out. The muscles were then excised and weighed on an analytical balance. The muscles were cut in two halves, placed on thin cork and then covered with Tissue-Tek II and immediately immersed in frozen isopentane (−160°C) supercooled with liquid nitrogen. Transverse sections 10 μm thick were cut in the belly region of each muscle on a cryostat (Bright Instruments Co.) at −25°C, these were collected on a clean slide and left to dry for 30 minutes at room temperature. The sections were then stored in a freezer (−10°C) until the time of staining.

1. MUSCLE FIBER TYPING

ATPase activity is believed to be closely related to the maximum rate of shortening of the muscle (Fitts & Holloszy 1977), therefore it can be used as an indicator of the different fiber types. Fiber differentiation and typing was therefore, carried out using the myosin ATPase method as described by Tunell & Hart (1977) with the procedure and pH modified for optimum staining results for the mouse and jerboa muscles. The pre-incubation and incubation media were prepared fresh for each run. Preincubation was in 0.1 mol glycine, 2% $CaCl_2$ and 10 ml of 40% fresh formalin made-up to 100 ml. The incubation media was 0.1 mol glycine, 2% $CaCl_2$ and 125 mg ATP disodium salt (Sigma). The procedure is outlined in Table 1. Adjacent sections were also stained for succinic dehydrogenase (Nachlas *et al.* 1957). The ATPase sections were cross referenced with the succinic dehydrogenase to confirm the typing of muscle fibers.

Table 1. Summary of histochemical procedure used to stain mouse and jerboa muscle for myosin ATPase.

Step	Parameter	mouse	jerboa
Pre-incubation Media	pH	7.25	7.2
	time (min)	10.0	35.0
	temp (°C)	25.0	25.0
Distilled Water (Wash)	time (s)	4×30	4×30
Incubation	pH	9.4	9.4
	time (min)	75.0	60.0
	temp (°C)	37.0	37.0
1% $CaCl_2$ (Wash)	time (s)	4×30	4×30
2% $CoCl_2$ (Immerse)	time (min)	3.0	3.0
Distilled Water (Wash)	time (s)	4×30	4×30
NH_4S (Immerse)	time (min)	1.0	1.0
Running Water	time (min)	10.0	10.0
Dehydrate in Alcohol	time (min)	1.0 each	1.0 each
Clear in Xylene	time (min)	2×1.0	2×1.0

2. MUSCLE FIBER NUMBER

ATPase stained sections were used to count the total fiber number of each fiber type. Since sections were cut in the belly region of each muscle and because of the simple geometry of the muscles used, virtually all the fibers are known to be present in these sections. Each counted fiber was allocated to one of the three fiber type categories; FOG, FG and SO. Total fiber number within each muscle was obtained by adding the individual fiber type numbers.

3. MUSCLE FIBER DIAMETER

The same sections were used to estimate fiber diameter as described earlier (Alnaqeeb & Goldspink 1987) on an Opton Photomicroscope III using an eyepiece graticule with a scaled cross-hair in the center calibrated for each magnification. Where possible, 100 fiber diameters were measured of each fiber type for each sex in each of 5 muscles of the EDL and the soleus.

4. STATISTICAL ANALYSIS

Data collected for fiber numbers were interpreted using Bartlett's test of homogeneity of variances and Tukey's test. Fiber diameter data was assumed to be affected by fiber type, the type of muscle in which it was found, the sex of the animal and the species of the animal. The highest level of classification was the species. The other variables fiber type, muscles type and sex were subclasses. Nested ANOVA was carried out to test whether there were differences between sexes or not, then the test was applied to the higher level; the species. The statistical programs SYSTAT (version 4.0 SYSTAT, Inc.) and STATGRAPHICS (STATGRAPHICS version 5.0 STSC Inc. and Statgraphics Co-op.) were used to compute statistical results.

RESULTS

1. MUSCLE WEIGHT

Calculated as a percentage of body weight the EDL muscle weight of male jerboas was greater than that of male mice (Table 2). In contrast female jerboas had an EDL

Table 2. Body weight (±SD), extensor digitorum longus (EDL) and soleus weight (±SD) of mice and jerboas.

Species	Sex	Body Weight g	EDL Weight		Soleus Weight	
			g	% body	g	% body
mouse	Female	34.83^{a3}	0.018^{*3}	5.17×10^{-4}	0.02^{*3}	5.74×10^{-4}
	$n = 6$	±4.99	±0.004		±0.01	
	Male	43.85^{a3}	0.026^{*3}	5.93×10^{-4}	0.032^{*3}	7.30×10^{-4}
	$n = 5$	±6.14	±0.009		±0.03	
jerboa	Female	60.04^{*3}	0.03^{13}	5.0×10^{-4}	0.038^{*2}	6.33×10^{-4}
	$n = 6$	±6.39	±0.01		±0.01	
	Male	56.16^{*3}	0.05^{13}	8.90×10^{-4}	0.04^{*2}	7.12×10^{-4}
	$n = 5$	±4.08	±0.01		±0.004	

n = number of muscles used.
* Probability between sexes within same species not significant.
[a] Probability between sexes within same species < 0.05.
[1] Probability between sexes within same species < 0.01.
[2] Probability between species not significant.
[3] Probability between species < 0.01.

percentage of body weight similar to that of female mice. On the other hand male mice and jerboa had similar soleus weights.

2. FIBER TYPE AND NUMBER

Mouse EDL had all three fiber types FOG, FG and SO. While jerboa EDL had only FOG and FG fibers (Fig. 1a). The total number of fibers in jerboa EDL muscle was three times higher than mouse (Table 3). Generally, although there were small differences in the number of different fiber types between sexes within the same species, these differences were not statistically significant.

The soleus muscle of mice also had all three fiber types FOG, FG and SO (Table 4). But the soleus of jerboa had FOG and SO fiber type only (Fig. 1b). Once again the total number of fibers in the jerboa was twice as high as that of mouse. In the soleus of both species, SO was the dominant fiber type.

Table 3. Mean fiber numbers (±SD) of the extensor digitorum longus (EDL) and the percentage of each fiber type (SO, FOG and FG) in female and male mouse and jerboa.

Species	Sex	SO Number & Percent	FOG Number & Percent	FG Number & Percent	Total Number & Percent
mouse	Female*	9 ± 7^{1}	436 ± 103^{2}	423 ± 84^{3}	869 ± 174
	$n = 5$	1.1%	50.1%	48.8%	100%
	Male*	9 ± 14^{1}	449 ± 154^{2}	498 ± 41^{3}	869 ± 174
	$n = 5$	0.9%	45.9%	53.2%	100%
jerboa	Female*	0.0	1803 ± 506^{2}	926 ± 187^{3}	869 ± 174
	$n = 5$	0.0%	65.5%	34.5%	100%
	Male*	0.0	1665 ± 322^{2}	1043 ± 209^{3}	2708 ± 458
	$n = 5$	0.0%	61.5%	38.5%	100%

n = number of muscles used.
* Probability between sexes within same species not significant.
[1] Probability between species < 0.001.
[2] Probability between species < 0.001.
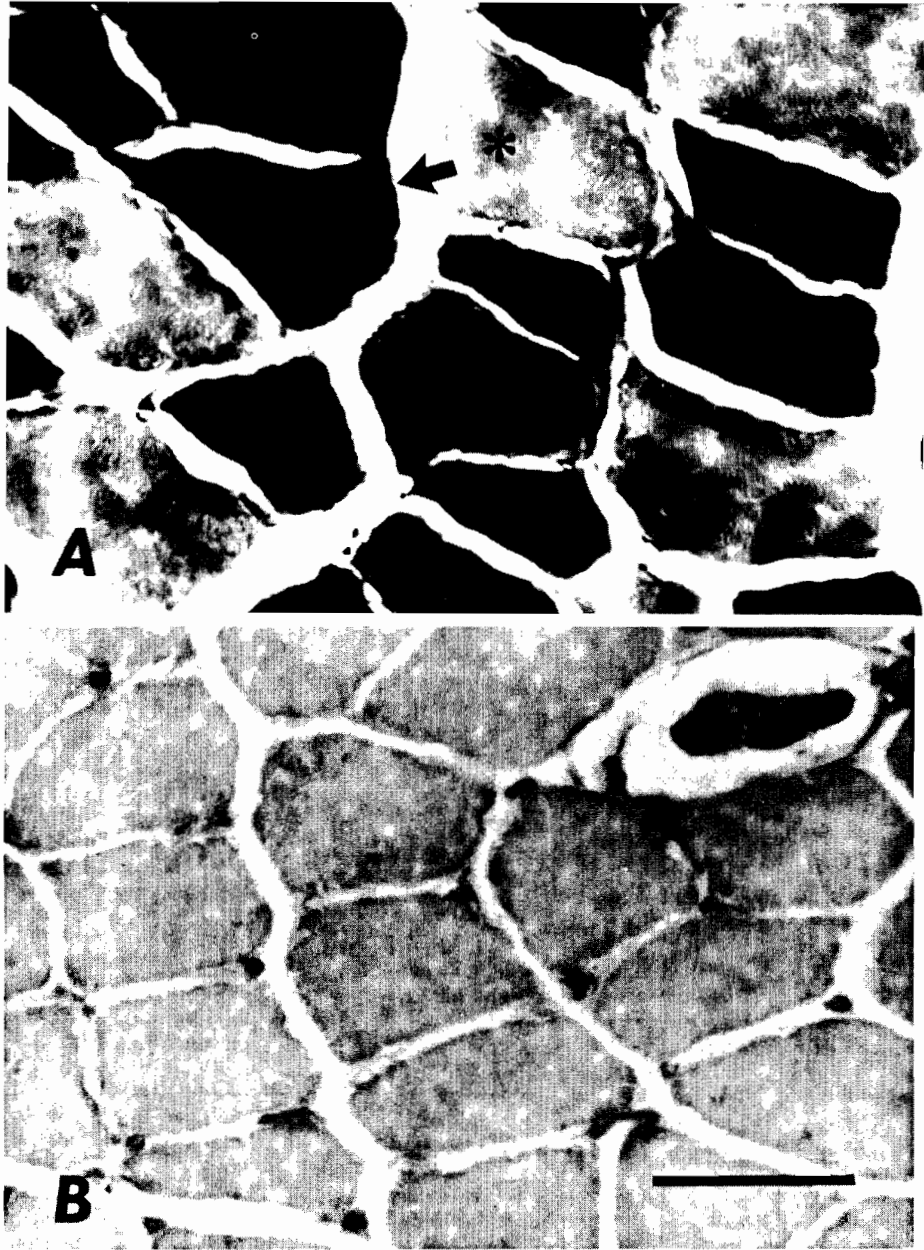[3] Probability between species < 0.001.

Fig. 1. Micrograph showing cross section in jerboa EDL muscle (a) where both FOG (←) and FG (∗) fibers are seen and in the soleus muscle (b) where only SO fibers exist. Size bar = 50 μm.

Because the two species had different body sizes and different total fiber counts per muscle, comparison between muscle fiber numbers of each type was carried out using fiber proportion in each muscle. The percentage of EDL FOG fibers in the jerboa was significantly greater than mouse (Table 3). This appears to be at the expense of FG

Table 4. Mean fiber number ($\pm$SD) of the soleus and the percentage of each fiber type (SO, FOG and FG) in male and female mouse and jerboa.

Species	Sex	SO Number & Percent	FOG Number & Percent	FG Number & Percent	Total Number & Percent
mouse	Female*	428 ± 122^1	294 ± 123^2	13 ± 27^3	735 ± 101
	$n = 5$	58.3%	40.0%	1.7%	100%
	Male*	414 ± 63^1	385 ± 54^2	2 ± 4.0^3	801 ± 53
	$n = 5$	51.6%	48.1%	0.2%	100%
jerboa	Female*	1864 ± 494^1	55 ± 77^2	0^3	1919 ± 504
	$n = 5$	97.3%	2.7%	0.0%	100%
	Male*	2032 ± 321^1	77 ± 108^2	0^3	2109 ± 383
	$n = 5$	96.7%	3.3%	0.0%	100%

n = number of muscles used.
* Probability between sexes within same species not significant.
[1] Probability between species < 0.001.
[2] Probability between species < 0.001.
[3] Probability between species < 0.001.

and SO fibers where FG and SO fibers were reduced in number, and SO fibers disappeared completely in the jerboa. The soleus of jerboa was dominated by SO fibers (Table 4) which were significantly more numerous than in mouse. In the soleus of the mouse, SO and FOG fibers shared dominance while FG fibers appeared least.

3. FIBER DIAMETER

ANOVA was used to analyze the fiber diameter measurement. Because of the complex nature of the data collected, the analysis took into account all the fiber diameters measured, including the variation introduced by muscle type and species. Both FOG and FG diameters in female mouse EDL were larger than males (Table 5).

Table 5. Comparison between FOG and FG fiber diameters (μm) of extensor digitorum longus (EDL) and SO fiber diameters (μm) of soleus in female and male mouse and jerboa.

Species	Sex	EDL FOG Diameter	EDL FG Diameter	soleus SO Diameter
mouse	Female	37.7 ± 7.5^1	54.7 ± 6.9^1	52.3 ± 8.9^1
	$n = 500$			
	Male	35.9 ± 8.5^1	38.6 ± 11.3^1	54.9 ± 9.6^1
	$n = 500$			
	Mean	$\mathbf{36.8 \pm 8.0^2}$	$\mathbf{46.7 \pm 12.9^3}$	$\mathbf{53.6 \pm 9.3^3}$
jerboa	Female	37.2 ± 6.6^1	$41.9 \pm 6.1^*$	45.0 ± 7.9^a
	$n = 500$			
	Male	35.4 ± 5.6^1	$41.7 \pm 4.9^*$	44.1 ± 6.5^a
	$n = 500$			
	Mean	$\mathbf{36.3 \pm 6.2^2}$	$\mathbf{41.8 \pm 5.5^3}$	$\mathbf{44.6 \pm 7.2^3}$

n = number of fibers of each type (100 fibers $\times$ 5 muscles).
* Probability between sexes within the same species not significant.
[a] Probability between sexes within same species < 0.05.
[1] Probability between sexes within same species < 0.001.
[2] Probability between species not significant.
[3] Probability between species < 0.001.

On the other hand, in the EDL, the SO diameters of males were larger than females in mouse.

In EDL FG fiber diameters were smaller in jerboas compared to mice (Table 3). Also, female mouse FG mean diameter was significantly larger than male, and significantly larger than jerboa of either sex. FOG fiber diameter of both species was essentially the same. In the soleus of jerboa SO fibers were of a smaller diameter than those of mice.

DISCUSSION

For a muscle to be versatile it has to contain several types of motor units with different intrinsic contraction speeds. The considerable variation in fatiguabilities of the different types of motor units has important physiological implication. It is known that fibers of different motor units intermingle, forcing their territories to overlap, this facilitates widespread contraction even on weak stimulation when only a few motor units are recruited (Edstrom & Kugelberg 1968; Goldspink 1981b).

SO motor units are stimulated by the lowest frequencies of all motor units and fatigue slowly making them efficient for posture maintenance. On the other hand, FG motor units fatigue almost completely after 3 minutes. FOG motor units are equipped with more oxidative enzymes and have higher mitochondrial densities but they are not capable of maintaining tension for long periods of time. Therefore, due to their slow recovery, FG and FOG motor units must be protected from continuous use by a high stimulation threshold, otherwise they will not be available when needed for strong and rapid movement.

The parameters of muscle weight, fiber number and fiber diameter are directly inter-related. Force production in muscle is proportional to fiber number multiplied by the cross-sectional area of the fibers. The observed results reflect an effect of the bipedal mode of locomotion on muscle composition.

The effect of bipedalism may be similar to that of high intensity training. Muscle weight in jerboa (calculated as a percentage of body weight) was higher compared to those of quadrupeds like the mouse. Male EDL was heavier in jerboa compared to mice. Also total fiber number in both muscles of jerboa was higher, with oxidative fibers FOG fibers in EDL and the SO in soleus predominating. The increase of FOG fibers can be attributed to the fact that fast fibers are better adapted for producing energy for fast movement of short duration (Tesch & Karlson 1985; Gonyea *et al.* 1986; Goubel & Marini 1987; Jansson *et al.* 1990) yet are more resistant to fatigue than FG fibers. Hather *et al.* (1991) noted an increase in FOG percentage and a decrease in FG fiber percentage in muscles of subjects under resistance training. Also sprint trained men showed a decrease in type I SO fibers from 57% to 48% and an increase in type IIA FOG fibers from 32% to 38% in thigh muscle biopsies (Jansson *et al.* 1990).

Diameter comparison between species showed significantly larger FG diameters in mouse EDL compared to jerboa. These findings suggest that jerboas do not use FG fibers as much when hopping but use instead FOG fibers. The latter are more fatigue resistance than FG fibers. Never-the-less FG fibers in jerboa EDL were larger in diameter than FOG in the same muscle, indicating that FG fibers are used when very fast and powerful movement is needed.

In rats trained to perform approximately 30 jumps/day for 8 weeks. Dooley *et al.*

(1990) noted that the fast medial gastrocnemius muscle showed a 15–18% increase in force production, and an increase in fatiguability (compared to controls) due to a 4% decrease in the percentage of type IIa FOG muscle fibers and a 6% increase of type IIab fibers, an intermediate fiber type between IIa FOG and IIb FG. The same investigators also demonstrated that the adaptations arise only when jumps exceed 30–50% of maximum height.

SO is the only fiber type common to the soleus of both species, SO fibers were small and dominated the whole of the jerboa muscle, this supports the idea that SO fibers here do not contribute to force production but rather specialize in posture maintenance. The presence of fast fibers in the mouse soleus indicate that it probably plays a secondary role in the animals locomotion in addition to its main role in posture maintenance. Dooley *et al.* (1990) noted that the soleus muscle did not show any change in fiber number, because it was thought to be less affected by vertical jumping compared to fast fibers in the medial gastrocnemius muscle but this was not in agreement with Pousson *et al.* (1991) who carried out a similar experiment, where they reported that rate soleus type I SO fibers decreased, while type II fast fibers; not specified increased. The two studies indicate that the presence of fast fibers is necessary for jumping and that the ratio of FOG to FG fiber numbers and the total cross-sectional area is a product of the force required and the desired fatigue resistance.

Kangaroos, although larger, but still bipedal, have equivalent muscle fiber composition to that of a jerboa. Their soleus muscle contains 100% SO fibers, and plantaris and gastrocnemius muscles are dominated by fast fibers with FOG fibers occupying the largest proportion. These adaptations are thought to give varying levels of fatigue resistance and indicate a considerable capacity for aerobic and anaerobic ATP production (Denington & Baldwin 1988).

The overall view suggests that the EDL muscle of jerboa is built to be fast, powerful and fatigue resistant. Where FOG fibers with their higher oxidative capacity contribute endurance, and FG fibers are only recruited when increased force is needed, especially with the proportionally large fiber area of FG to FOG fibers (Perry *et al.* 1988). On the other hand, soleus muscle of the jerboa showed more specialization for posture maintenance and more efficient use of energy. Hence SO fibers formed 97%, compared to less than 60% in the soleus of mouse.

EDL and soleus muscle fiber size and composition are consistent with the fiber recruitment pattern suggested by several authors (Rome *et al.* 1988; Armstrong 1981; Roy *et al.* 1991). The soleus muscle seems to be highly specialized for posture maintenance when the animal is standing still on its hindlegs or trotting whilst foraging. As the speed of hopping increases, FOG and FG fibers of EDL muscle may become engaged in force production because slow fibers cannot shorten fast enough to generate maximal jumps during running (Edstrom and Kugelberg 1968; Armstrong 1981; Roy *et al.* 1991).

In both muscles there appears to be a 'trade-off' between efficiency of the hindlimb muscular system and speed of contraction. Although slow muscles are more efficient in energy use and in maintenance of isometric tension (posture) for long periods of time, they are not suitable for production of fast powerful movement. In contrast to fast fibers, slow fibers become thermodynamically inefficient when contracting at speeds higher than their optimum rate of shortening (Goldspink 1981b; Rome *et al.* 1988) that is why they predominate in slow posture muscle. In addition, in muscles

where strong contractions are needed blood circulation in the muscle becomes compromised, fast motor units (FOG and FG units) are less affected because they depend on anaerobic metabolism and they will continue to provide power as needed during running (Edstrom & Kugelberg 1968; Armstrong 1981; Roy *et al.* 1991). It seems that the EDL and soleus in jerboa strike a balance between contraction speed, efficiency and fatigue resistance suited to their mode of locomotion.

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أنواع وعدد وحجم الألياف العضلية في عضلتي السوليس Soleus وأكستنسور ديجيتورم لونجس EDL في الجربوع.

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خلاصة

درست التحورات الناجمة من جراء الحركة بإستخدام الأرجل الخلفية في الجربوع Jaculus jaculus في عضلتي Soleus و EDL. وقد حللت أنواع الألياف العضلية وعددها وحجمها في العضلتين وقورنتا بمثيلتها في الفأر المخبري. غلبت الألياف العضلية من نوع FOG على تركيب EDL بينما غلبت الألياف العضلية من نوع SO على تركيب Soleus. أما الألياف العضلية فقد عكس مقدار الحمل الذي تتعرض له الألياف العضلية خلال الحركة. ويبدو أن نسب وأقطار الأنواع المختلفة من الألياف قد تأقلمتا مع طريقة المشي على الرجلين الخلفيتين. حيث كانت EDL مكونة من ألياف عضلية سريعة تعتمد على الطاقة الناتجة عن الأكسدة والتكسير المباشر للجلكوز بينما كانت Soleus مكونة من ألياف عضلية بطيئة تعتمد على الطاقة الناتجة عن الأكسدة فقط.