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Effect of immobilization and under-load on skeletal muscle in the Hindlimb of the Jerboa

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ABSTRACT

The jerboa *(Jaculus jaculus)* was used as a model of the bipedal mode of locomotion to study the effects of two immobilization positions on the extensor digitorum longus (EDL) and soleus muscles of the hindlimb. Cast immobilization was used to simulate the effect of disuse and hypo-activity on muscle properties. Fiber type, number and fiber diameter were examined to determine the effects of immobilization on the muscles. Immobilizing the EDL muscle in both stretched and relaxed positions caused atrophy and muscle wasting by reducing muscle fiber diameters. On the other hand, no significant changes in muscle fiber number were noted. The stretched soleus muscle, on the other hand, showed a significant increase in muscle fiber diameter, combined with a change from type I to type II fibers; furthermore, a significant decrease in the total fiber number was also noted. The relaxed soleus however, showed a significant reduction in muscle fiber diameter and number with no change in fiber type.

Keywords: Extensor digitorum longus; fiber size; fiber types; fiber number; immobilization; *Jaculus jaculus*; soleus.

INTRODUCTION

Muscles are key organs for providing the capability of movement to most living organisms. Studies, particularly in the skeletal muscle of vertebrates, have shown that these muscles contain populations of different types of muscle fibers. This enables skeletal muscle to produce a variety of contraction profiles both efficiently and economically (Goldspink 1981a). The final composition and appearance of striated skeletal muscle is influenced by several factors, such as gene activity (McComas 1996), age (Alnaqeeb & Goldspink 1987), central nervous control and activity, exercise (Fitts & Holloszy 1977) as well as lack of it imposed by plaster casts (Herbison *et al.* 1978), or denervation (Ansved & Larsson 1990) and overload (Asmussen & Soukup 1991).

Skeletal muscles may comprise a mixture containing all or some of a range of fiber types (Pearson & Young 1989). Fibers are classified as slow type I fibers which are high in oxidative enzymes and low in phosphorylase, and fast type II

fibers, with the reverse properties (Tunell & Hart 1977). Type I fibers are slow to respond to a stimulus and are also slow to contract. They contain large numbers of mitochondria and are responsible for maintaining posture and for carrying out slow, repetitive movements. Type II fibers can be divided into two subtypes. Type IIB fibers respond rapidly to a single stimulus. They have a very high intrinsic speed of shortening and a high myosin ATPase specific activity. These muscles have very few mitochondria and are used when rapid movement is required (Goldspink 1981b). Type IIA fibers are similar to type IIB fibers in their rate of contraction, although they have slightly slower intrinsic rates of shortening. They contain greater numbers of mitochondria than those found in IIB fibers, which makes them less subject to fatigue and able to recover more quickly from the effects of activity. Muscles containing type IIA fibers are adapted for fast, repetitive movements (Goldspink 1981b).

Skeletal muscle is known to demonstrate considerable morphological plasticity in response to exercise training. These adaptations include significant changes in muscle fiber size such as hypertrophy (Goldspink 1981b, 1985) and alteration in muscle fiber type composition (Fitts & Holloszy 1977, Fry *et al.* 1994). Weightlifting programs, for example, typically result in an increase in the cross sectional area of fast and slow fibers, although the greatest increase in size is usually seen in the fast fibers (Goldspink 1985, Cadefau *et al.* 1990). On the other hand, endurance training elicits a reduction in the muscle fiber cross sectional area (Goldspink 1981b). In contrast to strength training, endurance training produces well-defined, consistent changes in fiber types. Some of the type II fibers acquire the physiological, biochemical, and structural features of type I fibers; other fast fibers alter their myosin ATPase activity and convert from type IIB to type IIA (McComas 1996).

The most striking consequence of immobilization on muscle fibers is atrophy and a decrease in force-generating capacity. Effects of hypoactivity appear to be most profound in type I fibers, whereas the effects on type II fibers are less pronounced. There is also a tendency for type I fibers to be transformed into type II fibers, with attendant changes in the isoforms of the myofibrillar proteins (McComas 1996). Additionally, at the surface of the immobilized muscles, the motor units show abnormal signs of degeneration and reduction in the diameter of the large myelinated nerve fibers (Malathi & Batmanabana 1983); this in turn causes effects similar to ones observed in denervation.

The jerboa *(Jaculus jaculus)* is a member of the family Dipodidae, which are

characterised by their remarkable adaptations for jumping. Their hind legs are up to four times the length of the front legs (Nowak 1991). When moving rapidly, jerboas leap and spring with their hind legs, covering up to three meters in a single bound. When moving slowly, they use only their hind legs in a bipedal walk; at both speeds the tail is used as a balancing organ (Nowak 1991). The bipedal mode of locomotion in jerboas is believed to have a great influence on the physiological and biochemical properties of the hindlimb muscles. The effect of bipedalism may be similar to that of high intensity training in some respects. The similarities are in the increased weight of the hindlimb muscles in bipedal animals like kangaroos (Dennington & Baldwin 1988) and jerboas (Alnaqeeb & Al-Baker 1994) as well as in the unique composition of fibers in the fast and slow muscles of such models in comparison with quadrupedal animals of similar weights. Al-Baker (1992) demonstrated that the EDL muscle of jerboas is built to be fast and powerful, and as a result it is dominated by IIA fibers representing 64% of the total fiber number with their high oxidative capacity, and relatively high recruitment. In comparison, IIA fibers in the mouse account for only 50%. The soleus muscle on the other hand, showed more specialisation for posture maintenance with type I fibers accounting for 97% of the fibers, whereas in the mouse soleus they accounted for 56% of the total fibers (Al-Baker 1992).

In the present study we examined the changes that occured as a result of enforced inactivity. In the jerboa the normal mode of movement (jumping) and enforced inactivity are at the extreme ends of the spectrum of muscle activity. The morphological and morphometric changes that occur as a result of inactivity give insight into the importance of maintaining muscular activity.

MATERIALS AND METHODS

Animals

Wild jerboas were collected from Subiyah desert area, 60 kilometers to the north of Kuwait City. Healthy female animals, ranging in weight from 40-60g, were chosen. Throughout the study the animals were kept in the animal house at a constant temperature (20-22°C) and relative humidity (40-50%). Water and food were available *ad libitum*. The diet during the period of acclimatization consisted of rodent diet (Aliment Pour, UAR, France) in its commercial form, ground and mixed with flour and baked into bread. Later, and for the duration of the experiment, the animals where switched to the full commercial diet. Initially, thirty adult females were divided into three groups each consisting of 10 animals for each experiment. Each group of animals surviving treatment were divided

equally and randomly, and half of the animals were used for this part of the study. Wherever necessary, experimental animals were anesthetized during application of the cast using 2.5% sodium thiopentone (May & Baker, England), 25μg/100g body weight, using intraperitoneal injections. Using plaster casts applied to the knee and ankle joints, the hindlimb was immobilized in one of two positions. In the first group, the right hindlimb was immobilized at about 180° by stretching it almost straight at the knee joint (tibia and femur in a straight line), and the calcaneus was at about 90° to the tibia. This position results in the stretching of the EDL and the relaxation of the soleus. The right hindlimb of animals in the second group was immobilized so that the leg was in a position approximating sitting, where the calcaneus and tibia were at about 30° angle and the knee joint was at the resting position at about 45° angle. In this position the EDL is relaxed and the soleus is stretched. The third group was used as a control, where the limbs were left free.

Animals in the three groups were sacrificed by urethane overdose after three weeks. Each muscle was then excised as close to the bone as possible, and cut into pieces. Two pieces from the belly region were placed on a piece of cork in such a way that both supported each other with their long axis perpendicular to the cork. The pieces were then covered with Tissue-Tek II, and immediately immersed in super-cooled iso-pentane cooled with liquid nitrogen. Sections were cut at 10 μm in a cryostat cooled to -20° C. Sections were collected on pre-washed clean slides at room temperature; slides were left to dry for 30 minutes, then stored in a freezer at - 40° C prior to staining.

Staining

Fiber differentiation and typing was performed using the myosin ATPase method described by Tunell & Hart (1977), with the pH modified for optimum staining results for jerboa muscle fibers (Alnaqeeb & Al-Baker 1994). The stock solutions of the pre-incubation media were prepared by dissolving 0.75g glycine and 0.585g of NaCl in 800ml of distilled water which was then made up to 1l. $CaCl_2$ (0.75M) was prepared by dissolving 11.03g $CaCl_2$ in100ml distilled water. Fresh formalin (40%) was prepared by heating 60ml of distilled water up to 70° C, then adding 40g of paraformaldehyde while stirring. The volume of the solution was then adjusted to 100ml by adding distilled water, then it was filtered and stored. Finally, NaOH (0.1M) was prepared by dissolving 40g of NaOH in 1l of distilled water.

The pre-incubation medium was prepared fresh by mixing 100ml of stock pre-incubation medium with 20ml of $CaCl_2$ and while stirring 13ml of fresh formalin was slowly added. The solution was adjusted to pH 7.25 at room temperature by adding approximately 7ml of 0.1M NaOH. The incubation medium was

prepared by mixing 100ml of stock pre-incubation medium with 20ml of $CaCl_2$. The pH was adjusted to approximately 9.35 using 12ml of 0.1M NaOH; to that 0.16g of ATP disodium salt (Sigma, USA) was added and stirred until completely dissolved. Then the pH was readjusted at room temperature, and the solution was placed in a water bath at 37°C. The staining was performed as shown in Table 1. Haematoxylin and eosin stains were used routinely to examine sections from both muscles and all treatments.

Table 1. Summary of histochemical procedure used for myosin ATPase staining.

Step	Parameter	
Pre-incubation temp medium	pH	7.25
	time (min)	1-5
	temp (°C)	room temperature
Distilled water	time (s)	2x30
Incubation medium	pH	9.4
	time (min)	60
	temp (°C)	37°C
1% $CaCl_2$ (wash)	time (s)	2x30
2% $CoCl_2$ (immerse)	time (min)	3
Normal saline	time (s)	2x3
NH_4S (immerse)	time (min)	1
Running water	time (min)	5
Dehydrate in alcohol series	time (min)	2 each
Clear in xylene	time (min)	2x2

Muscle fiber type identification, fiber number and diameter

Following the ATPase staining procedure, muscle fibers were classified into types I, IIA and IIB using a binocular photo microscope (Vanox, Olympus) attached to a video camera (Sanyo, Japan). Several images were obtained to cover the whole area of the muscle section. The fiber number for each fiber type was determined by counting the fibers totally enclosed within each frame and the fibers touching the top and left edges of the frame. The number of fibers in the frames was totalled for each fiber type in each muscle. The total fiber number was obtained by adding up the different fiber types belonging to the same muscle.

Muscle fiber diameter was measured as the mean of the two orthogonal diameters (Schmitt 1976) using an image processor (Quantimat 520, Cambridge Instruments, UK), connected to a Vanox microscope (Olympus, Japan) system and a CCD video camera (Sanyo, Japan). A total of 100 fibers were measured for each fiber type in each muscle.

Statistical Analysis

Data collected for muscle fiber numbers were interpreted using SPSS for Windows (Ver. 7.5.1, SPSS Inc.) applying the two sample t-test. The t-test was applied when only the means of two samples were compared, as when comparing the fiber number of relaxed EDL muscle with the fiber number of the control EDL muscle. As for fiber diameter measurements, the statistical results were computed with Statgraphic Plus for Windows (Ver. 1.0, Manugistics Inc.) using the analysis of variance (ANOVA). The ANOVA test was applied when the comparisons were made between multiple groups or groups that contained subsets of data, such as when fiber diameter data were compared in each group of animals for each treatment.

RESULTS

Fiber type identification

Using myosin ATPase staining, fiber types I, IIA and IIB could be distinguished. In the control EDL muscle only two types of muscle fibers could be seen (type IIA and IIB, Fig. 1a). In the stretched EDL muscle, types IIA and IIB could be seen in addition to type I fibers (which were only three muscle fibers) to which no statistics could be applied (Fig. 1b). The relaxed EDL muscle showed the same types of fibers as seen in the control, namely type IIA and IIB fibers (Fig. 1c).

The control soleus muscle as well as the relaxed soleus were made up entirely of the pale type I fibers. The slightly darker appearance of some sections (Fig. 2a) was due to the longer incubation time of the soleus. The stretched soleus muscle, on the other hand, had two fiber types, the dark type II fibers and the pale type I fibers (Fig. 2c). Both immobilization positions showed degenerating fibers which were more abundant in the stretched position. Degenerating fibers were identified using haematoxylin and eosin stained sections. Degenerating fibers had central nuclei, irregular appearance and shape.

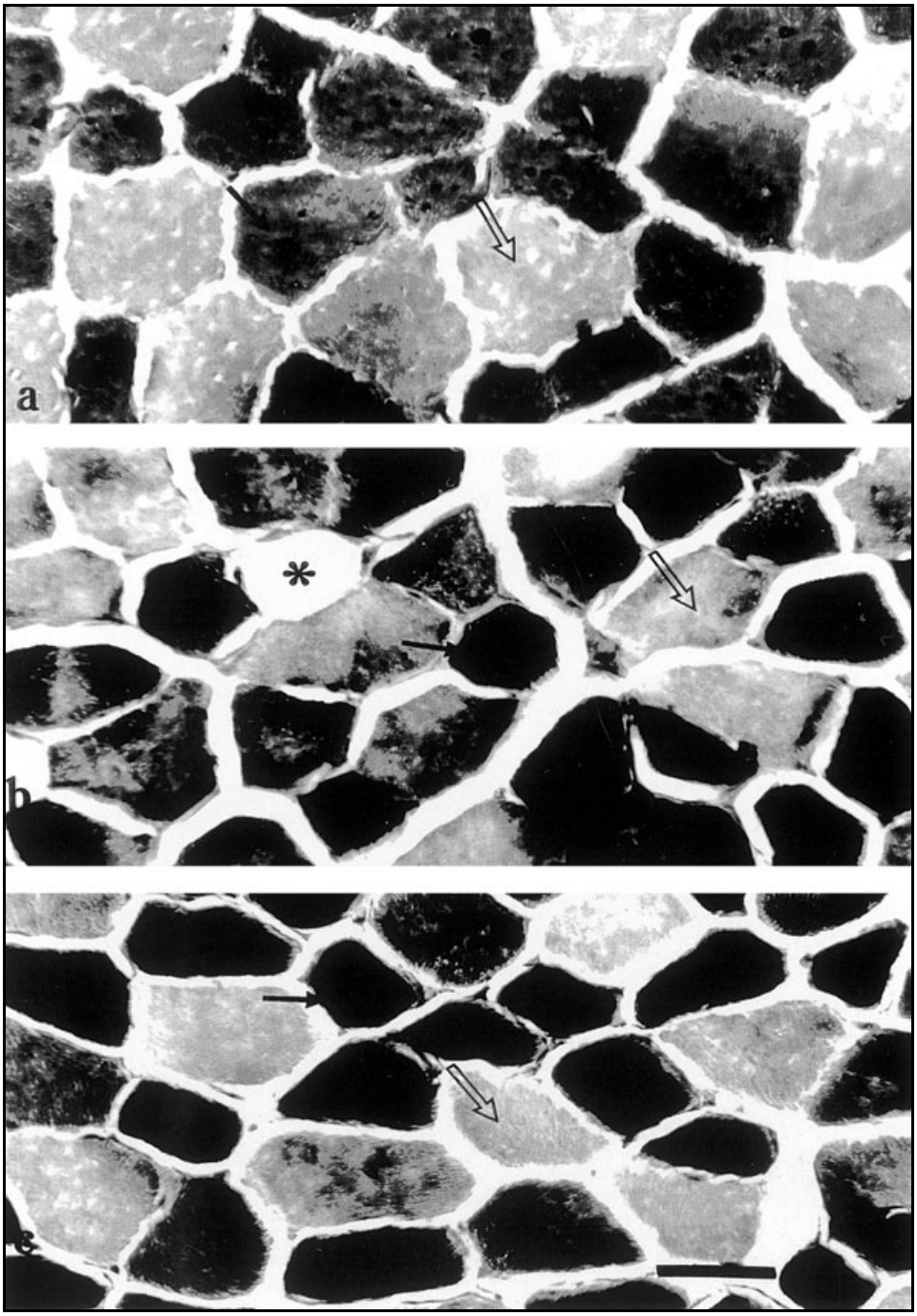

Fig.1: EDL muscle stained for myosin ATPase. (a) Control muscle (➔) indicates type IIA while (⇨) indicates type IIB. (b) Stretched EDL muscle showing fiber type IIA (➔), fiber type IIB (➨) and fiber type I (*). (c) Relaxed EDL muscle appeared similar to control with only type IIA (➔) and type IIB (⇨). Size bar = 70 μm.

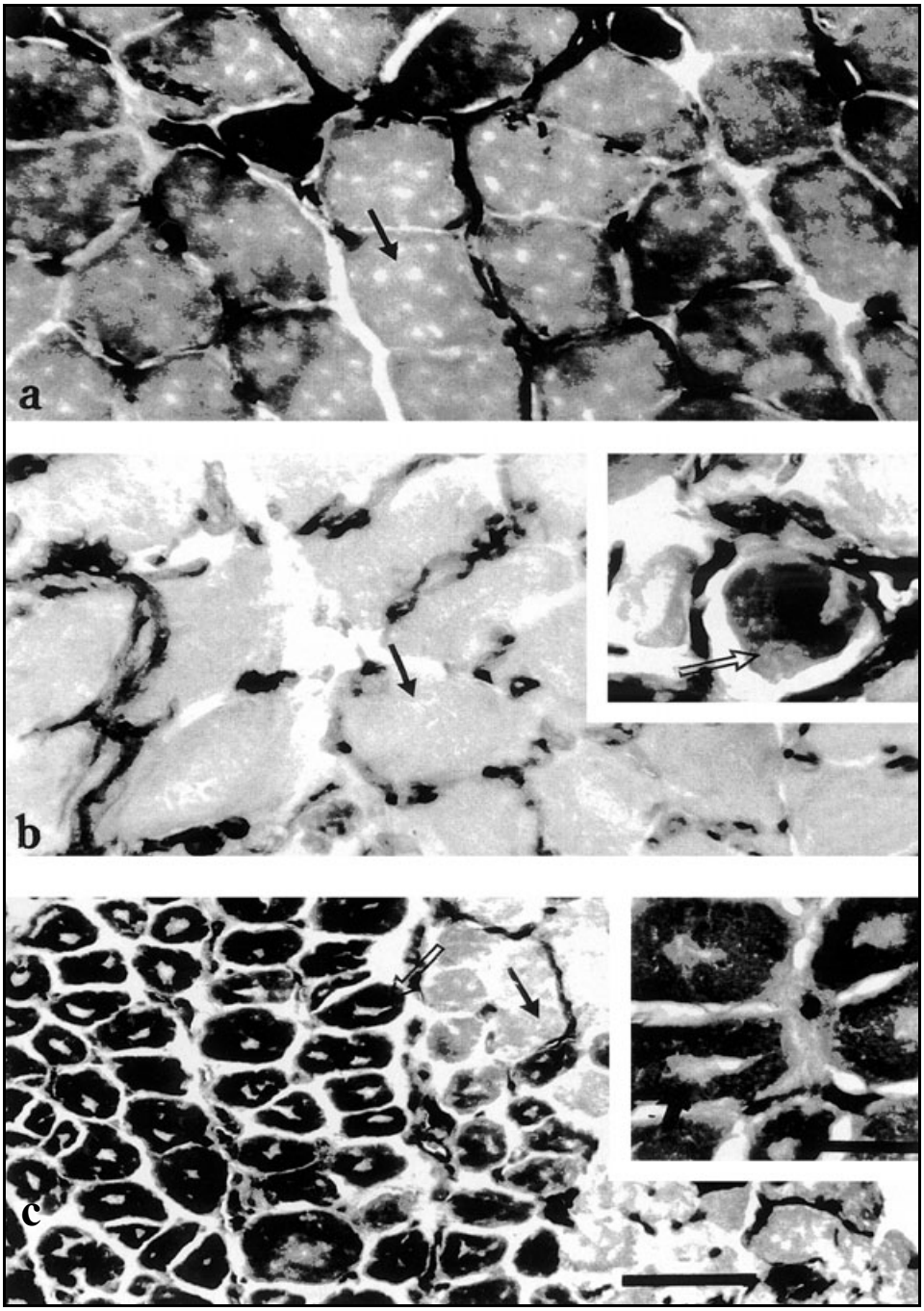

Fig.2: Soleus muscle stained for myosin ATPase. (a) Control muscle had only the pale type I fibers as shown (➔). (b) Relaxed soleus muscle showing fiber type I (➔); the insert shows a degenerating muscle fiber (⇨). (c) In the stretched soleus muscle two types of muscle fibers were observed, types I (➔) and II (⇨). The insert shows magnified type II fibers (➨) (note the presence of central nuclei). Size bar = 70 μm. Insert size bar = 30 μm.

Muscle fiber number

The total fiber number in the two immobilization positions of the EDL muscle, stretched and relaxed EDL muscle, did not change significantly when compared to the control EDL muscle (Table 2). Although there were fluctuations in both IIA and IIB fiber number in both immobilization positions, neither was statistically significant (Table 2).

Table 2. Type IIA and type IIB fiber numbers, total number of fibers and percentage of each type in control, stretched and relaxed EDL muscle.

Treatment	Fiber number Mean ± SD Percentage		
(n = 4)	Type IIA	Type IIB	Total IIA + IIB
Control	643.7 ± 161	896.8 ± 60.5	1540 ±202
	(41.4 ± 5)	(58.7 ± 5)	
Stretched	710† ± 105.3	726† ± 82.6	1436 ± 180
	(49.4 ± 2.1)	(50.7 ± 2.1)	
Relaxed	529.5†± 55.4	785.3† ± 58.5	1314 ± 109
	(40.2 ± 1.6)	(59.8 ± 5)	

† = not significant when compared to corresponding control
n = number of animals

In the soleus, both control and relaxed muscles showed only type I fibers (Table 3). On the other hand, the stretched soleus muscle showed two types of muscle fibers, the slow type I and the fast type II. When comparing the means of both immobilization positions with the control, the relaxed soleus muscle showed a reduction in total fiber number while the stretched soleus showed both a reduction in fiber number and a shift in fiber type I to type II.

Table 3. Fiber number in control, stretched and relaxed soleus muscle.

Treatment	fiber number (Mean ± SD)		
(n = 4)	Type I fiber	Type II fiber	Total Fiber number
Control	1548 ± 82	-	1548 ± 82
Stretched	906* ±168	378 ± 43	1284* ± 164
Relaxed	998* ±106	-	998* ±106

* = $P \leq 0.05$
n = number of animals

Fiber diameter measurements

The mean fiber diameter of type IIA fibers in the control EDL (32.5μm) was higher than that of both stretched and relaxed muscles by 14.2% and 4.6%, respectively (Table 4). Furthermore, the stretched EDL muscle showed a greater reduction in the size of fiber diameter, implying that the stretching of a muscle affected the diameter of IIA fibers more than relaxing it. A significant difference was shown in the data collected for type IIB fibers when compared to the control (Table 4). Type IIB mean fiber diameter of stretched muscle (20 μm) was reduced in size by 20.9% when compared to the control. The type IIB fibers in the relaxed position were only reduced by 13.8% compared to control.

Table 4. Comparison of fiber diameters in control, stretched and relaxed EDL and soleus muscles.

Treatment (n = 4)	Fiber Diameter (μm) (Mean $\pm$ SD) EDL		Soleus
	Type IIA	Type IIB	Type I
Control	32.5 $\pm$ 4.5	25.3 $\pm$ 5.7	32.3 $\pm$ 6.2
Stretched	27.9* $\pm$ 5.7	20.0* $\pm$ 4.1	38.4* $\pm$ 6.1
Relaxed	31.0* $\pm$ 5.6	21.8* $\pm$ 3.6	27.4* $\pm$ 5.4

* = $P \leq 0.05$
n = number of animals

The fiber diameter of type I fibers in the stretched soleus muscle was higher than that of the control by 15.9% (Table 4). As for the relaxed soleus muscle, a reduction of 15.2% in fiber diameter was shown when compared to the control.

DISCUSSION

For a muscle to be versatile, it should contain several types of motor units with different intrinsic contraction speeds. The considerable variation in fatigabilities of the different types of motor units has important physiological implications. It is well known that fibers of different motor units intermingle forcing their territories to overlap, which facilitates widespread contraction even on weak stimulation when only a few motor units are recruited (Edstrom & Kugelberg 1968, Goldspink 1981a). The bipedal mode of locomotion may be considered a type of enforced high intensity exercise, which in some respects affects the composition of muscles. Several studies on humans have revealed that an increase in the strength of a muscle is correlated with an enlargement of the muscle bulk, especially of fast-twitch fibers, after 12 weeks of training

(Hakkinen *et al*. 1985, Rutherford & Jones 1986). The enlargement appears to be in response to an increased workload. The hindlimbs of bipedal animals have to support the whole body weight continually and are the major muscles for locomotion (Goldspink 1977).

The changes of histochemical profiles of the fast EDL muscle and the slow soleus muscle were studied against changes in fiber type, number and diameter. These parameters are usually studied when investigating the degree of atrophy in a particular muscle since they are related directly to muscle performance. Just over half of the fibers in the EDL muscle of jerboa were type IIB fibers, characterized by low oxidative capacity and high myosin ATPase activity. These fibers are recruited when very rapid movement is required such as when evading a predator. The remainder of the muscle is made of type IIA fibers, in which the combination of the high respiratory capacity and the high myosin ATPase activity allows these fibers to contract rapidly, yet remain less fatigable. Accordingly, the EDL muscle of the jerboa is designed to perform fast and sustained activity by recruiting the two fast fiber types (IIA and IIB) as required.

The present study showed a shift towards the dominance of type IIB fiber number (58.7% in control EDL muscle) over type IIA fiber number (41.3%), contrasting the earlier findings of Alnaqeeb & Al-Baker (1994) which showed 34.5% of type IIB fibers to 65.5% of type IIA fibers in control EDL muscle. This may have resulted from the enforced caging of the animals for a longer period in the present study, between three to five weeks prior to the experiments, thus reducing their normal movement and affecting the ratios of the different fiber types in the muscle. As for the two immobilization positions of the EDL muscle, no significant changes in muscle fiber numbers or ratios were found in the EDL muscle.

Alnaqeeb & Al-Baker (1994) reported that the soleus muscle of the jerboa was dominated by type I fibers. This is in agreement with the findings of the present study for both the control and the relaxed soleus muscle. The stretched soleus muscle, however, had a different profile; up to 30% of the fibers in some muscles were of type II fibers.

The diameters of type I fibers were significantly increased in the stretched soleus muscle and reduced in the relaxed muscle when compared to the control. This is in agreement with results obtained in the soleus of quadrupedal animals such as rats, where both type I and II fibers decreased in diameter in neutral casted animals (Herbison 1978) and increased in relation to overload (Roy *et al*. 1985). However, total fiber number in both the stretched and relaxed soleus

showed a significant decrease compared to the controls. This is not surprising in relaxed muscles, since atrophy is common in unloaded, immobilized muscles. The decrease in fiber number in stretched muscle, on the other hand, is unusual. The decrease appears to be associated with a transformation from type I to type II fibers and an increase in degenerating fibers as indicated by the observed central nucleii (Fig. 2c). Combined, the two observations indicate an overload situation. Studies on myosin heavy chain (MHC) expression in immobilized stretched rat muscle have shown a reduction in the expression of both type I and IIA MHC genes and an increase in the expression of embryonic MHC genes (Loughna *et al.* 1990). Our observations indicate a loss of fibers due to degeneration followed by regeneration. This is manifested in the pattern of dark fibers observed in the stretched soleus (Fig. 2c).

Imposing muscle restriction in the form of immobilization on both EDL and soleus muscles showed that soleus muscle is highly plastic when compared to the EDL muscle affected by these same factors. The morphological and structural changes in the soleus muscle are considered adaptations to an imposed condition as compared to the normal situation. When the soleus muscle is stretched, significant changes occur at the muscle fiber level, such as fiber diameter increase and fiber type transformation. These changes indicate that the soleus muscle was adapting to an increased workload by changing the fiber composition to a higher-force producing type, which in spite of having higher energy expenditure, is still resistant to fatigue. That contradicts the role of the soleus muscle as a tonic muscle used for posture maintenance. On the other hand, the relaxed soleus muscle underwent great changes as a result of shortening the muscle to a less-than-normal length. A significant reduction in fiber diameter and number occurred as a response to muscle disuse.

It is clear from the present study that the unique musculature of the hindlimb of the jerboa was affected by enforced inactivity of the normally highly active, jumping animal. Although the fast EDL exhibited some changes caused by the inactivity, the slow soleus was by far more affected by immobilization, especially when subjected to stretch immobilization. Immobilization positions may be used to advantage in order to reduce the effect of inactivity on a muscle, especially in muscles that are normally less active.

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تأثير عدم الحركة وتخفيف الحمل على عضلات الرجل الخلفية للجربوع

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خلاصة

الجربوع (جاكيولوس جاكيولوس) حيوان ثنائي الأرجل استخدم كنموذج لدراسة تأثير وضعين مختلفين من عدم الحركة على كل من عضلة (EDL) وعضلة (Soleus) في الرجل الخلفية للجربوع.

باستخدام جبيرة على أرجل الحيوانات تحت الدراسة، تم منع حركتها لمحاكاة أثر الخمول ونقص النشاط على خصائص العضلة ومن ثم تحديد المجموع الكلي للألياف العضلية وأنواعها وأحجامها لمعرفة آثار عدم الحركة على العضلات.

وقد تبين من الدراسة أن تأثير عدم الحركة على عضلة (EDL) في وضعي الشد والاسترخاء قد تسبب في ضمور العضلة وهزالها نتيجة للنقص الملحوظ في أحجام الألياف العضلية على الرغم من عدم وجود أي تغير إحصائي في عدد هذه الألياف.

أما بالنسبة لعضلة (Soleus) في وضعية الشد لوحظ زيادة في حجم الألياف العضلية مقرونة بتحول بعض هذه الألياف من الألياف البطيئة (I) إلى الألياف السريعة (II) مع نقص في عددها الكلي. أما في حالة الاسترخاء فتبين وجود نقص واضح في أحجام الألياف العضلية بالإضافة إلى عددها الكلي مع عدم تغير نوع هذه الألياف.