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EFFECTS OF PROLONGED JUMP TRAINING ON FIBERS' DISTRIBUTION AND FAT CONTENT IN RABBIT SKELETAL MUSCLE

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ABSTRACT

EFFECTS OF PROLONGED JUMP TRAINING ON FIBERS' DISTRIBUTION AND FAT CONTENT IN RABBIT SKELETAL MUSCLE. **Ducomps C. Rémignon H. Doutreloux JP. Lebas F. Mauriège P. JEP**online. 2004;7(1):27-36. Thirty male rabbits were jump-trained during 15 weeks to investigate the effects of exercise on muscle fiber distribution and morphology and intramuscular adipocytes. Our study classified Extensor Digitorum Longus (EDL) and Rectus Femoris (RF) as fast-twitch mixed muscles, and confirmed the slow-twitch oxidative and fast-twitch glycolytic types of Semimembranosus proprius (SMP) and Psoas Major (PSOAS) respectively. PSOAS muscle displayed a strong decrease in IIA fibers and an increase in IIX+IIB fibers with aging ($0.001 < P < 0.05$), whereas muscle fiber distributions remained stable in EDL, RF and SMP muscles. In response to jump training, the percentage of type IIA fibers in RF or PSOAS muscles was significantly higher in trained compared to control animals at each age (respectively $P < 0.05$ and $P < 0.001$), whereas the percentage of IIX+IIB fibers was lower in trained rabbits ($P < 0.05$). Few significant changes were found in fiber cross-sectional areas. The surface area of perivascular adipocytes was significantly lower in all trained muscles at 90 and 140 days ($0.001<P<0.05$). These results highlight the phenomenon of muscular plasticity and show that jump training increases the percentage and SDH activity of oxidative and glycolytic IIA fibers in fast-twitch mixed (RF) or glycolytic (PSOAS) muscles, without a measurable muscular hypertrophy. The number of IIA fibers rises via a conversion of IIX+IIB fibers, which, concerning PSOAS muscle, delays its mature metabolism. Finally, jump training seems to be able to activate lipid metabolism.

Key Words: fiber types, high intensity exercise, plasticity, adipocytes.

INTRODUCTION

Most of the fibers in rabbit skeletal muscles can be classified into one of the four principal fiber types (I, IIA, IIX or IID, IIB) using a histochemical classification (1). This classification derives from Brooke & Kaiser (1970) and was completed with the characterization of IIX or IID fibers. These principal fiber types were confirmed by complementary techniques, notably electrophoresis, which permitted the isolation and identification of Myosin Heavy Chain isoforms (MHC) (1). The existence of a phenomenon of interconversion of muscle fibers (i.e. changes from type IIB into type IIA and then into type I and vice versa) has already been demonstrated by chronic low or high-electrical stimulation in rat and rabbit (3,4).

Exercise training is also known to act on morphological, biochemical and histochemical characteristics of muscle fibers, these effects of exercise training being now well documented, particularly in the case of endurance training (5,6). A long-duration endurance program seems to reduce the percentage of type IIB fibers while increasing the percentage of type IIA fibers in human skeletal muscles (7). Indeed, the percentage of type IIB fibers is known to decrease at the advantage of type IIX and IIA fibers (8,5). The conversion of type IIA fibers into type I fibers has also been reported, this phenomenon remaining, however, difficult to reproduce in physiological conditions (7). Endurance training does not appear to induce a rise in the cross sectional area of muscular fibers, and previous studies even mentioned a reduction in fiber size (5,6). The most conspicuous effect reported concerning high-resistance training was an increase in the cross sectional area of the main muscle fiber types (9,10).

In the case of high-intensity exercise training, an increase in the percentage of type IIA fibers has already been reported in humans in response to sprint training (12). This increase in the percentage of type IIA fibers could result from a possible conversion of type IIB fibers into type IIA fibers (11). Cadefau *et al.* (1990) also found an increase in both the percentage of type I fibers and the diameter of type I and II fibers. To the best of our knowledge, only very few studies until now have dealt with the adaptation of rat muscle to jump training (14,15). The results of these studies showed an increase in the percentage of type IIA fibers and a decrease in the percentage of type I fibers in soleus muscle (14). Watt *et al.* (1982) had also mentioned a decrease in the percentage of type IIB fibers coupled with an increase in type IIA fibers in fast-twitch muscles.

Finally, as mentioned above, the effects of endurance exercise training are well known on muscle fibers, likewise on adipocytes and lipid metabolism; that is exactly the contrary with high intensity exercise training. Thus, it would be relevant to know if a high intensity exercise training like jump training could affect the percentage of fibers by the phenomenon of conversion.

The aim of this study was therefore to examine the effects of a long-term jump-training program on both the distribution of fibers types by histochemical typing and their morphology by measurement of the fiber cross sectional areas, this to highlight the phenomenon of muscular plasticity. This analysis was completed by an evaluation of the impact of jump training on the adipocytes and lipid metabolism. The rabbit was chosen as the animal model since it displays a natural aptitude to jump.

METHODS

Animals

Sixty hybrid male rabbits (White New Zealand Rabbits 1077) were purchased from the Institut National de la Recherche Agronomique (INRA, Toulouse, France). Each animal was initially subjected to a general physical examination by a qualified technician and any rabbit deemed abnormal was excluded from the study. During the study period, rabbits were housed in a climate-controlled room at an ambient temperature of 20±2°C, under a regimen of 12 h of light/day (lights on 7 am).

Rabbits were cared and handled in conformity with the *'European convention for the protection of vertebrate animals used for experimental and other scientific purpose'*. Food (Rablo Formax, Alisud, containing 60 % carbohydrate, 17 % protein, 3 % fat, and 14 % cellulose) and water were provided ad libitum throughout the study.

Training Protocol

Sixty weaned male rabbits (31 days old) were randomly assigned to two groups of 30 animals: a sedentary control group and an exercise-trained one. Control rabbits (C) were housed individually in standard cages limiting their possibilities of movements, while trained animals (T) were three per large cages (length: 2.13m, width: 0.62m, height: 0.80m). These large cages were equipped with two gates, thus dividing the cage in three equal volumes. The gates were equipped with an obstacle adjustable in height (Figure 1).

Trained rabbits had to jump over these obstacles to have access to food and water, which were located at each side of the cage. The height of obstacles was determined according to the animal size and age, as indicated in Table 1.

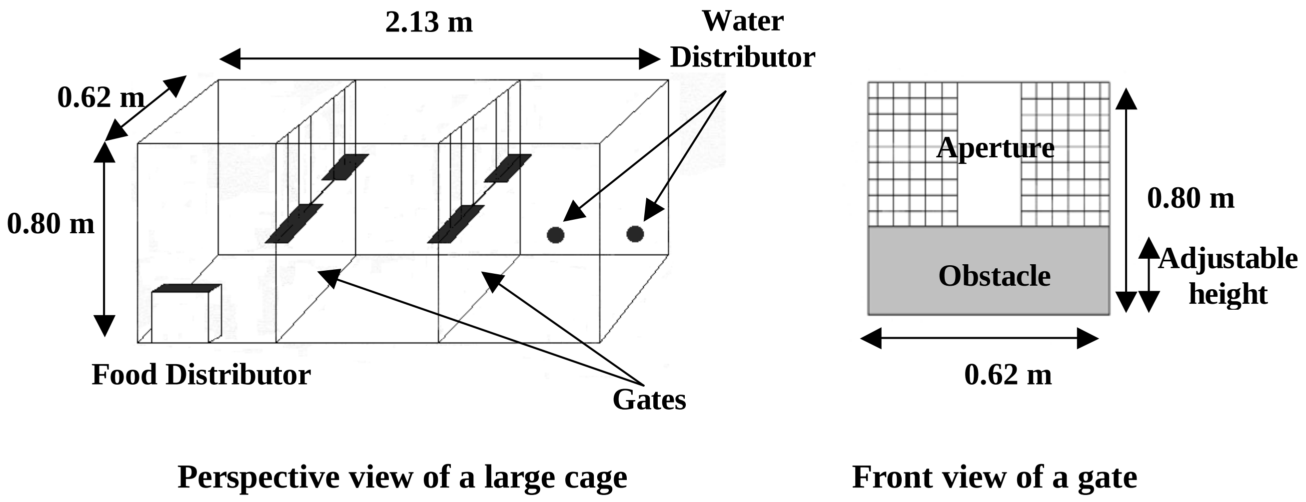

Figure 1. Illustration of a large cage equipped with two gates comprising an obstacle adjustable in height.

A video monitoring was carried out over a 24 h period with highly sensitive cameras (allowing recording during the dark phase, only requiring the extremely low light diffused by the camera light), in order to count the number of jumps achieved by all trained rabbits, one day before sacrifice occurring at 50, 90 and 140 days. 10 control and 10 trained animals were killed at these different ages. 140 days of age corresponds to sexual maturity and end of growth in rabbits (16). Animals with injuries (hematomas, muscular lesion, etc.) were all excluded from the study.

Table 1. Height of the obstacles at different stages of age.

Animals' age	*Height of obstacles*
30 to 50 days	0.25 m
51 to 90 days	0.30 m
91 to 110 days	0.35 m
111 to 140 days	0.50 m

Histochemical and Morphological Analysis

Serial cross-sections (14 µm thick) of**:** Extensor Digitorum Longus (EDL), Rectus Femoris (RF), Semimembranosus Proprius (SMP), PSOAS Major (PSOAS) muscles from both control (C) and trained (T) rabbits were cut on a microtome in a cryostat at -20° C. The sections were taken from the midsection of the muscles, then air-dried during 1 hour, and subsequently stained. Sections were taken from five muscles of each type, per group and per age. Three sections from each sample were stained to reveal myofibrillar actomyosin ATPase. ATPase activity of the different fiber types was assessed by pre-incubation at pH 4.3, 4.6 or 9.4, respectively 10 min, 30 min and 1 h at ambient temperature (17). Fibers were classified in type I, IIA and IIX+IIB, a classification that was derived from Brooke & Kaiser (1970). One additional serial section of each sample was stained to measure succinic dehydrogenase (SDH) activity, an indicator of the potential intensity of oxidative metabolism (18). The muscle samples of the trained and control animals were placed on the same slide, to rule out the possibility of artifact differences between fibers, resulting from the histochemical process.

After staining, the percentage and the mean cross-sectional area (CSA) of the different fiber types were determined on approximately 200 fibers in three random fields for each section, using a computerized image analysis system (RACINE) (19). This software requires clear identification of inter-fiber network and stained myofibers, supplied by another section stained with red azorubin.

Other sections were stained with Oil red-Kristallviolet, to color in red/orange intramuscular adipocytes. This staining allows determining the surface area occupied by adipocytes around a vessel in the section, using the software Visilog® 5 (Noesis, Québec, Canada). Results were expressed in μm^2 of surface occupied by adipocytes around a vessel.

Statistical Analyses

Values are presented as means ± standard deviation (SD). Data were analyzed by a two-way (age, training) analysis of variance with post hoc tests (Student's t test), using SPSS®. Statistical significance was defined at $P<0.05$.

RESULTS

The anthropometric data revealed no significant differences between T and C animal muscle and body weights at the three stages of age. The mean body weights of T and C animals were respectively 1722±150 and 1779±141 g at 50 days, 3073±222 and 3082±239 g at 90 days, and 4013±344 and 4074±169 g at 140 days. During experimentation one trained rabbit died and three presented muscular, osseous and joint lesions on their rear limb. Some rabbits presented muscular hematomas, probably due to torn muscles. Video tapes revealed an average of 90±9, 180±13 and 60±5 jumps/trained rabbits in the large cages during a 24 hour period (12 hours of dark phase and 12 hours of light phase), at 50, 90 and 140 days of age, respectively (see Figure 2).

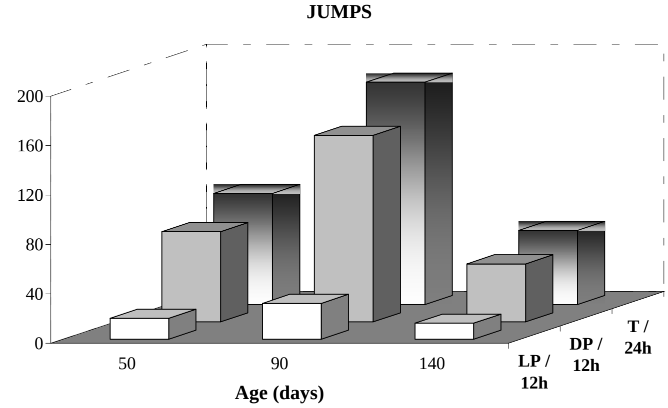

Figure 2. Average of jumps performed per trained rabbit during a period of 24 hours (T) composed of 12-hour light (LP) and dark phases (DP). The number of jumps performed during the dark phase highlights this phase as being the principal period of activity for the rabbit.

Muscle Characteristics and Fiber Distributions

EDL and RF are fast-twitch muscles, containing about 90-95% of type II fibers, in the C group. EDL muscle displayed similar percentages of IIA and IIX+IIB fibers, whereas RF muscle showed a higher proportion of type IIX+IIB fibers. PSOAS is a fast-twitch glycolytic muscle only containing type II fibers, with a large proportion of IIX+IIB fibers (~90%) in the C group, at 140 days. SMP is a pure slow-twitch oxidative muscle, exclusively containing type I fibers from 50 days in both groups.

Fibers distribution in EDL and RF muscles remained relatively stable with ageing particularly in C rabbits, in contrast to PSOAS muscle which displayed a strong decrease in IIA fibers and an increase in IIX+IIB fibers in both groups ($0.001<P<0.05$, Figure 3).

The percentage of type I fibers in EDL muscle increased in T compared to C group at 90 and 140 days ($P < 0.05$, not shown). As illustrated by Figure 3, the percentage of IIA fibers in RF muscle was 21 to 31 % higher in the T than in the C group at the three stages of age ($P<0.05$). Figure 4 highlights the higher activity of SDH in IIA fibers and therefore oxidative metabolism in trained RF trained muscles. The increase in IIA fibers in RF muscle was accompanied by a proportionate reduction in IIX+IIB fibers, at 50 and 90 days of age ($P<0.05$, Figure 3).

Finally, the percentage of IIA fibers in PSOAS muscle was 56 to 109 % higher in T compared to C rabbits, at the three stages of age ($P<0.001$, Figure 3), whereas the percentage of IIB fibers was lower in T than in C rabbits at 50 and 90 days ($P<0.05$, Figure 3).

Muscle Fiber Cross Sectional Area (CSA)

The cross sectional area of muscle fibers increased significantly with age between 50 and 140 days in all muscles and groups ($P<0.001$, Table 2). However, there was very little significant difference in the CSA of all muscles between T and C rabbits at the three stages of age (Table 2). The relative CSA (calculated) confirmed the increasing in the surface represented by type IIA fibers in both RF and PSOAS muscles in T animals at 90 and 140 days ($0.01<P<0.05$, not shown).

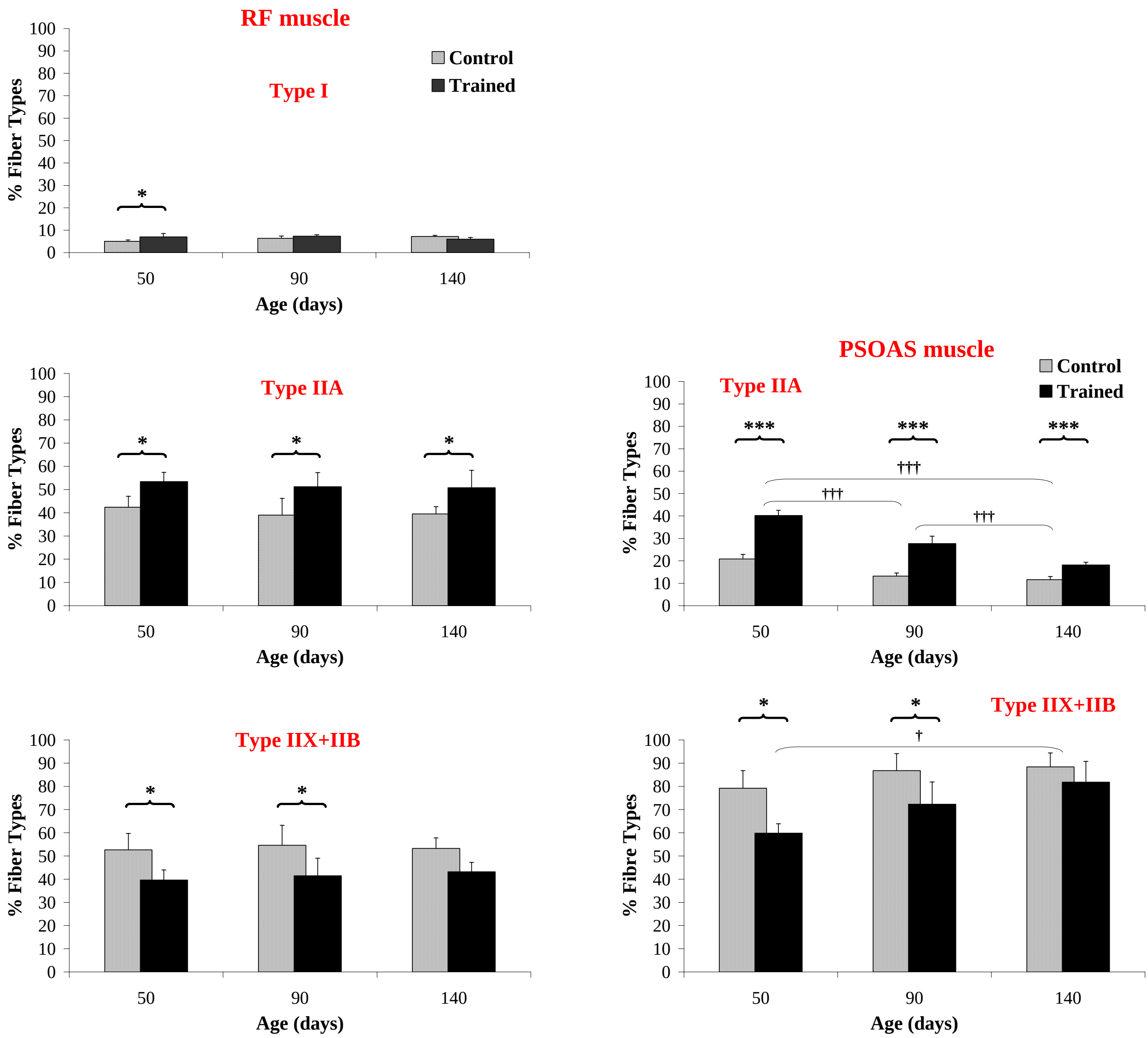

Figure 3. Fiber type distribution (%) of RF and PSOAS muscles from control and trained groups at 50, 90 and 140 days. Values are means±SD, n= 5 muscles per group and per age. Significant difference between groups of similar age at * P<0.05, ** P<0.01 and ***P<0.001. Significant increase with age in T and C group at † P<0.05 (†† P<0.01, ††† P<0.001, NS non significant).

Surface Area Occupied by Perivascular Adipocytes

Fast-twitch mixed and glycolytic muscles such as EDL, RF and PSOAS displayed a significantly lower surface occupied by perivascular adipocytes than the slow-twitch oxidative muscle SMP, in both groups at 90 and 140 days (0.001<P<0.05). As illustrated in Table 3, whatever the group and the muscle considered, the average surface rose significantly with age, between 50 and 140 days (P<0.001). Finally, for each muscle considered, the mean surface occupied by adipocytes differed between groups; it was lower in T muscles, compared to C ones, at 90 and 140 days (0.001<P<0.05, Table 3).

Table 2. Fiber cross sectional area (CSA, µm2) of EDL, RF, SMP and PSOAS muscles, from control (C) and trained (T) groups at 50, 90 and 140 days.

		I		IIA		IIB+IIX	
MUSCLES	AGE	T	C	T	C	T	C
	50	1764±281	1496±419	1905±323	1825±397	3293±618	2912±499
EDL	90	2095±440	1873±475	2260±546	2092±597	3555±865	3218±766
	140	2536±716§	2201±486†	2729±429§	2489±412†	5161±772§	5088±732†
	50	1798±346*	1078±227	1696±292	1398±257	2939±465	2573±484
RF	90	2512±606	2241±210	3464±604	2807±661	5175±768	4808±913
	140	2716±605§	2432±599†	3637±624§	3321±625†	5739±940§	5202±819†
	50	1736±276	1656±334				
SMP	90	3440±844	3248±641				
	140	3620±854§	3888±876†				
	50			1135±176*	869±101	1373±374	1148±228
PSO	90			1583±365	1466±353	2622±621	2538±670
	140			1534±306§	1709±245†	2835±610§	2917±648†

*Values are means±SD, n=5 muscles per group and per age. Significant difference between groups for a muscle considered at similar age at * P < 0.05. Significant difference with age between 50 and 140 days for each muscle considered of T (§ P < 0.001) and C groups († P<0.001).*

Table 3. Surface area occupied by adipocytes in sections of EDL, RF, SMP and PSOAS muscles, from trained and control groups at 50, 90 and 140 days.

				SIGNIFICANT LEVEL	
MUSCLES	AGE	TRAINED	CONTROL	GROUP[1]	AGE[2]
	50	3581±993[a]	3286±804[a]	NS	
EDL	90	2960±513[b]	8220±1928[c]	***	***
	140	7853±1570[c]	12469±2023[d]	**	
	50	9038±1855[a]	10613±2428[a]	NS	
RF	90	10083±1963[a]	19806±4071[b]	***	***
	140	23831±4869[b]	29010±5263[c]	*	
	50	7016±1387[a]	11391±2062[b]	**	
SMP	90	19294±3744[b]	28194±4681[c]	**	***
	140	34250±6166[c]	44011±8019[d]	*	
	50	2482±443[a]	7519±1568[b]	***	
PSOAS	90	5816±1043[b]	12569±2112[d]	***	***
	140	8776±1814[c]	15967±3120[d]	***	

Values are means ± SD, n= 5 muscles per group and per age. [abcd] For each muscle in a same line or column, values with different letters differ significantly. Significant difference: [1] between T and C groups of similar age, [2] with age between 50 and 140 days in T and C groups at NS: non significant, * P<0.05, ** P < 0.01 and *** P < 0.001.

DISCUSSION

To the best of our knowledge, our study is the first one that used different muscle types and the rabbit as an animal model in a jump-training program. Indeed, the mode of training chosen in our study was rarely used and corresponds to a high intensity exercise (14). Rabbits were stimulated to jump by the presence of food according to their own rhythm of dark-light activity. It is also interesting to note that this training mode is more respectful of the animal circadian biorhythm as rabbits do not perform jumps under constraint. Nevertheless, the presence of muscular lesions and the great frequency of jumps carried out by trained animals, compared notably to Pousson *et al.* (14), highlight the intensity of stimulation, characteristic of high intensity exercise.

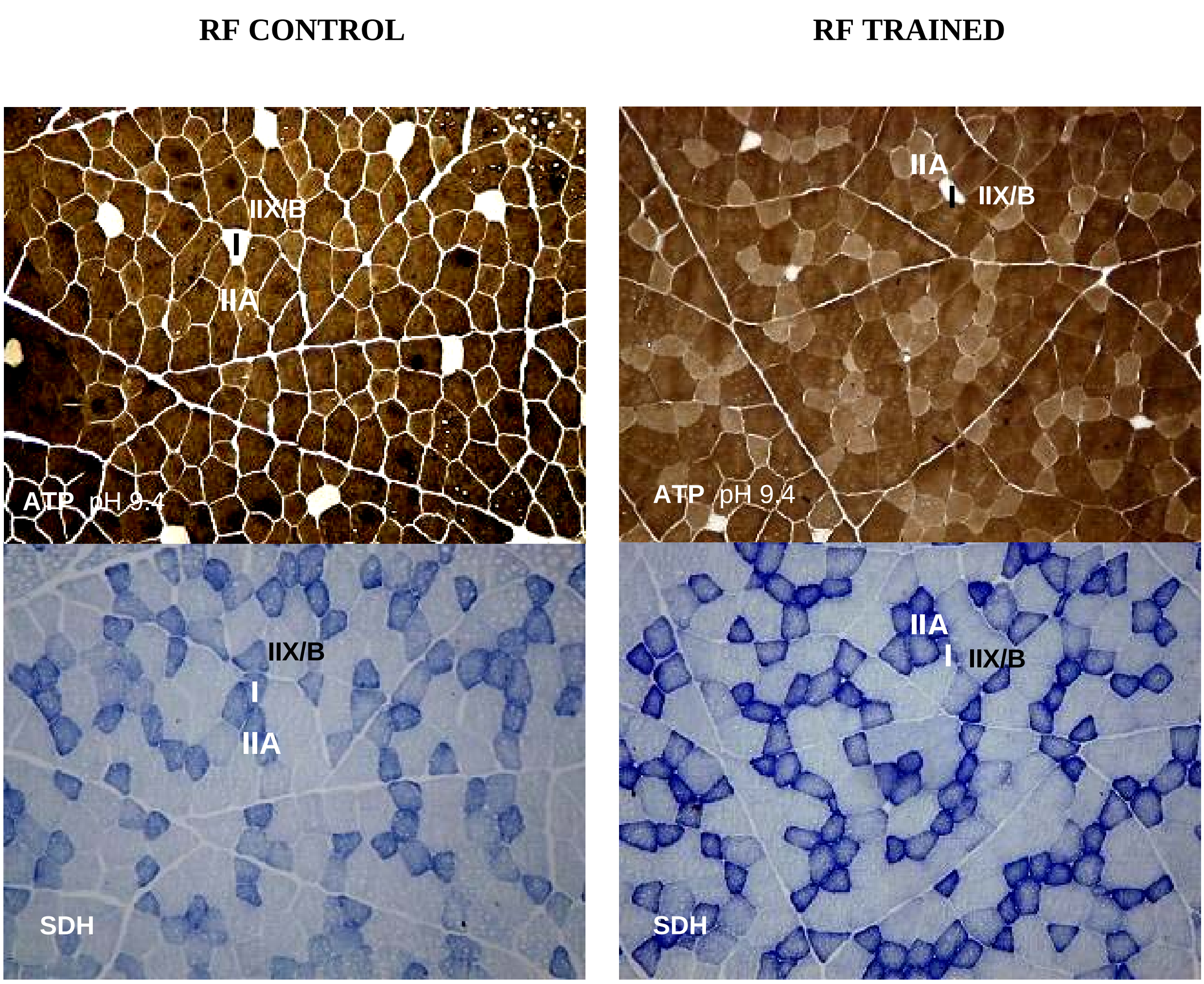

Figure 4. Histochemical analysis of serial cross-sections of Rectus femoris (RF) muscles after treatment at 140 days. These serial sections were stained to reveal myofibrillar actomyosin ATPase (ATP) and succinic dehydrogenase (SDH) activities in RF muscles of a control and a trained rabbit.

In this study, we have chosen to use the old method of Brooke & Kaiser (2) completed with SDH activity to determine the type of fibers and their metabolism, because these methods remain very simple and the information is sufficient to highlight the effects of exercise training. However, although these techniques do not allow to discriminate accurately between IIX and IIB fibers (contrary to electrophoresis of MHC isoforms), it is important to note that previous studies have shown that in rabbit fast-twitch muscles such as EDL or PSOAS, MHC-IIX isoform is predominant compared to MHC-IIB isoform which only represents 0 to 2 percent of total MHC isoforms (20,21,22). Moreover, our results are in accordance with these previous studies and confirm the fast-twitch type of EDL and PSOAS muscles and respectively their mixed and glycolytic metabolism (1,21,22). Concerning SMP muscle, it represents an excellent model of slow-twitch muscle with a pure oxidative metabolism (23). As for RF muscle, it displays fast-twitch mixed properties but tends to be more glycolytic than EDL.

In our study, the percentage of contractile fibers remained stable with age in EDL and RF muscles of the control group, and more particularly in SMP muscle. On the contrary, PSOAS presents a strongly varying typology with age in both groups, as IIA fibers decrease and IIX+IIB fibers increase, thus leading the muscle to its glycolytic profile. These results confirm those of previous studies according to which SMP muscle only expressed type I myosin from the end of weaning, and concerning glycolytic muscles such as PSOAS, the late acquisition of mature metabolism after the contractile differentiation (24,16).

High intensity exercise changes the distribution of all muscle fibers, while preferentially modifying fast-twitch ones, such as type II fibers (11,25). Our results show that jump training affects the distribution of fibers in EDL muscle by increasing the percentage of type I fibers. This can be due to the high level of stimulation reached by this muscle in this exercise type. RF muscle which is strongly involved as the principal extensor of the knee in the phases of impulse and reception (eccentric contraction), displays a significant reduction in IIX+IIB fibers, coupled with a rise of IIA fibers. This finding probably corresponds to a conversion of glycolytic IIX+IIB fibers into oxidative and glycolytic IIA fibers in fast-twitch RF muscles of T animals. Moreover, there is an increase of SDH activity and therefore of oxidative metabolism in RF muscles of T animals. These results are concordant with previous studies using high intensity exercise training (11,15) or resistance training (9,10). As for SMP muscle, it did not display any change in fiber type, probably because it is only composed of type I fibers and seems to have achieved a complete maturation from 30-35 days onwards (i.e. the beginning of training). PSOAS muscle of T animals shows at the three stages of age, a higher percentage of IIA fibers to the detriment of IIX+IIB fibers, compared to C animals. However, the evolution with age is similar to sedentary animals' muscles whose number of IIX+IIB fibers increases. It seems that in case of PSOAS muscle, jump training is likely to delay the evolution towards the adult "glycolytic" stage.

The cross sectional area (CSA) of type I, IIA and IIX+IIB muscle fibers increases with age (i.e. during growth), but this type of training does not seem to involve a real hypertrophy of fibers because there are few significant differences in the CSA between groups. This type of finding concerning the CSA of fibers was already mentioned in a study using high intensity exercise training (11), these results differ, however, from other experiments where an increase in the CSA was detected after jump or sprint (13,15).

The reason for this discrepancy is not clear; although it may be partially ascribed to the estimation of the distribution of muscle fibers, as in humans only few and superficial fibers are generally studied (11). However, in our case, it is possible that the type of training using preferably IIA fibers –which are less involved in muscular hypertrophy than glycolytic fibers such as IIX or IIB– has relatively less impact on the morphology.

As intramuscular lipid content is low in rabbits, measurements of the surfaces occupied by adipocytes were made around blood vessels, where they are essentially located. These surfaces increase with the animals' age between 50 and 140 days, which is in agreement with previous observations on bovines (26) and pigs (27). This rise in intramuscular lipids is due to an increase in the number and surface area of the adipocytes, but can also vary according to the muscle considered. Indeed, the glycolytic PSOAS and mixed EDL and RF muscles display lower surfaces of perivascular adipocytes, compared to the oxidative SMP muscle. Alasnier et al. (1996) mentioned concordant data concerning the higher lipid content in oxidative muscles like the SMP. Our results point out a significant reduction of the surface occupied by the intramuscular adipocytes in muscles of T animals, compared to C rabbits. This important finding highlights the fact that jump training such as jumping can act on the lipid metabolism.

CONCLUSIONS

These results highlight the muscular plasticity phenomenon and confirm that jump training is able to induce numerous muscle adaptations. Jump-training increases type I fibers in EDL muscle, and principally the percentage of oxidative and glycolytic type IIA fibers by a conversion of type IIX+IIB fibers in fast-twitch mixed and glycolytic muscles (RF, PSOAS), thus delaying the acquisition of mature metabolism for the glycolytic PSOAS muscle. This type of training clearly seems to promote the oxidative metabolism, illustrated by a higher SDH activity, particularly in fast-twitch type IIA fibers. However, jump-training induces only little variations in the cross sectional areas of the different fiber types of the four muscles studied. Nevertheless, jump training is able to reduce the intramuscular lipid content and seems to activate lipid metabolism.

Further, it would be relevant to verify the effects of this exercise type on humans, particularly on muscle fiber type distributions and also to examine if high intensity exercise training is likely to stimulate human lipid metabolism compared with endurance training.

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