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The effect of nutrition on the size and proportion of muscle fibre types during growth

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ABSTRACT

To investigate whether the retardation in the increase of body weight produced by reduced food intake could influence the transformation of muscle fibre types in soleus and extensor digitorum longus (EDL) during growth, rats were divided into 3 groups at 3 wk of age. Each group was subjected to food restriction from 3 wk of age to the following ages. Group 1 comprised 5 (148.7±7.3 g), 7 (250.7±11.1 g), 9 (362.9±19.3 g) and 11-wk-old rats (414.9±35.2 g) fed ad libitum. Group 2 comprised 5 (148.7±7.3 g), 7 (148.6±7.7 g), 9 (147.7±6.0 g) and 11-wk-old rats (148.8±5.7 g) fed a restricted diet; these animals were similar in weight to the 5-wk-old rats in group 1. Group 3 comprised 4 subgroups of 11-wk-old rats (148.7±5.7 g, 247.6±6.8 g, 354.4±8.6 g, 414.4±35.2 g); their body weights were adjusted to the weights of 5, 7, 9 and 11-wk-old rats in group 1 by restriction of food intake. Muscle weights and fibre areas in soleus and EDL significantly increased with growth. The muscle weights and fibre areas in group 2 in which body weights were equal increased significantly with age, but the increases were significantly less than for group 1. The muscle weights and fibre areas in group 3 in which ages were equal increased significantly with increasing body weight; the increases were the same as those in group 1.

Percentages of type I fibres in soleus and type IIB fibres in EDL changed significantly with growth. The percentages also changed with age in group 2, but did not alter with increasing body weight in group 3. There were significant relationships between the muscle fibre types of soleus and EDL and body weight in group 1, but the relationships did not emerge in group 3. It is concluded that the increase in muscle weight and fibre area from 5 to 11-wk-old rats is mainly influenced by the degree of food restriction, but that the transformation of muscle fibre types is not modified by factors associated with food restriction.

INTRODUCTION

Several workers have investigated the changes in the distribution of muscle fibre types during postnatal growth in most mammalian species (Brooke et al. 1971; Tomanek, 1975; Curless & Nelson, 1976; Kugelberg, 1976). It has been suggested that a number of factors may be correlated with fibre differentiation in the first few weeks of postnatal growth, including innervation (Rubinstein & Kelly, 1978; Gambke et al. 1983; Vrbová et al. 1985), stretching and overloading of muscles (Lowrie et al. 1989), and thyroxine levels (Gambke et al. 1983; Butler-Browne et al. 1984; Sugie & Verity, 1985). It has been reported that the innervation of the rat soleus muscle is established by 4 wk (Brown et al. 1976) and the basic activity pattern of the muscle by this time already resembles that of the adult muscle (Vrbová et al. 1985). However, the distribution of muscle fibre types changes continuously after this stage (Tomanek, 1975; Smith et al. 1988). Furthermore, there have been no investigations into the relationship between thyroid hormones and the transformation of muscle fibre types after 4 wk. It thus appears that there is no definitive evidence as to the factors that cause transformation of muscle fibre types after this stage.

Kugelberg (1976) reported the existence of a close relationship between muscle fibre types and body

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Table. *Body weight and age in each group*

	Subgroup 1	Subgroup 2	Subgroup 3	Subgroup 4
	Group 1			
Age (wk)	5	7	9	11
B.W. (g)	148.7±7.3	250.7±11.1*	362.9±19.3*†	414.9±35.2*†‡
	Group 2			
Age (wk)	5	7	9	11
B.W. (g)	148.7±7.3	148.6±7.7§	147.7±6.0§	148.8±5.7§
	Group 3			
Age (wk)	11	11	11	11
B.W. (g)	148.8±5.7	247.6±6.8*	354.4±8.6*†	414.9±35.2*†‡

Values are means±S.D. * Different from subgroup 1; † different from subgroup 2; ‡ different from subgroup 3; § different from group 1.

weight. He argued that the increases in leg length and body weight increase the demand for slower motor units and diminish it for fast units, and that this induces the redistribution of muscle fibre types. Other investigators have also reported a strong correlation between muscle fibre type and body weight (Sillau & Banchero, 1977; Ripoll et al. 1979; Aquin et al. 1980; Tamaki, 1985). It has been reported that tenotomy, a model for overloading the synergists, accelerates the decrease in type IIA fibres in the synergists (Tomanek, 1975; Watt et al. 1984). In addition, it has been reported that suspension, a model for unloading the hindlimb, decreases the proportion of type I fibres (Elder & McComas, 1987). These results raise the possibility that the increase in body weight with growth is responsible for the overloading of muscles, thus causing the redistribution of muscle fibre types.

In this study we investigate whether a retardation in the increase in body weight produced by reduced food intake modifies the transformation of muscle fibre types between 5 and 11-wk-old rats.

MATERIALS AND METHODS

Male Wistar rats were used. The rats were divided into 3 groups at 3 wk of age (43.4±2.2 g). Each group was subjected to food restriction from 3 wk of age to the following ages. The first group (group 1) comprised 5, 7, 9 and 11-wk-old rats fed ad libitum (7–8 rats per subgroup). Group 2 comprised 5, 7, 9 and 11-wk-old rats comparable in weight to the 5-wk-old rats in group 1 as a result of restricted food intake (7 rats per subgroup). Group 3 comprised 4 subgroups of 11-wk-old rats. Their body weights were adjusted to the 5, 7, 9 and 11-wk-old rats in group 1 by restricting the food intake (7–8 rats per subgroup). The final body weights and ages of each subgroup in groups 1 to 3 are shown in the Table. The rats in group 1 were fed ad libitum (Oriental Yeast Co. Ltd, rat chow). The rats in groups 2 and 3 with reduced food intake were pair-fed an identical diet to adjust their weights to those of the corresponding subgroups in group 1. As each subgroup 1 in groups 1 and 2, each subgroup 4 in groups 1 and 3, and subgroup 4 in group 2 and subgroup 1 in group 3 received the same food intake protocol, subgroups 1 and 4 in group 1 and subgroup 4 in group 2 were substituted for subgroup 1 in group 2 and subgroups 4 and 1 in group 3. All the rats were weighed at 3–4 d intervals from the age of 3 wk. If the weights of the rats in groups 1 and 2 at this time differed from the weight assumed from the last target weight, their food intake was changed. This manipulation maintained a positive weight change and avoided rapid increases. All rats were housed in separate cages (14×20 cm for 3 to 7-wk-old, 14×30 cm for 7 to 11-wk-old) in a constant-temperature room (22±2 °C) with free access to water.

Soleus and extensor digitorum longus (EDL) muscles were rapidly dissected and freed of fat and connective tissues, and the wet weights were recorded. The muscles were then cut transversely at their widest point and immediately frozen in isopentane cooled to −130 °C with liquid nitrogen. Each tissue sample was cut into 10 μm thick serial sections in a cryostat at −20 °C. For the identification of muscle fibre types, tissue slices were processed by myofibrillar actomyosin ATPase after preincubation (room temperature) for 4 min at pH 4.3 and 4.6, and for 10 min at pH 10.3 (Gollnick et al. 1983). Muscle fibres were classified as type I, IIA, IIB and IIC according to the nomenclature system of Brooke & Kaiser (1970). To ensure adequate sampling, fibre type composition was determined by counting ~ 1200 fibres from the middle portion of the cross-section in each muscle. Fibre area was determined from a section stained with ATPase (pH 4.6) by projecting the slide and tracing fibre borders with a digitiser connected to a personal

computer. If possible, areas of more than 50 fibres of each type were measured in each muscle. Because only a small proportion of type IIC fibres was found, they were not included in the analysis.

Standard statistical procedures were employed to calculate the means and standard deviations. One-way and two-way ANOVA was used for comparison between the subgroups in a group and for comparisons of the corresponding subgroups between groups. For all statistical tests, differences between means were regarded as significant when a value of $P < 0.05$ was obtained.

RESULTS

Muscle weights and fibre areas

Figure 1 shows changes in muscle weights for soleus and EDL with age in groups 1 and 2. Each muscle weight increased significantly with age in groups 1 and 2. Muscle weights for soleus and EDL of 7, 9 and 11-wk-old rats in group 2 were significantly less than those in group 1 ($P < 0.05$).

Changes in muscle weights of soleus and EDL with

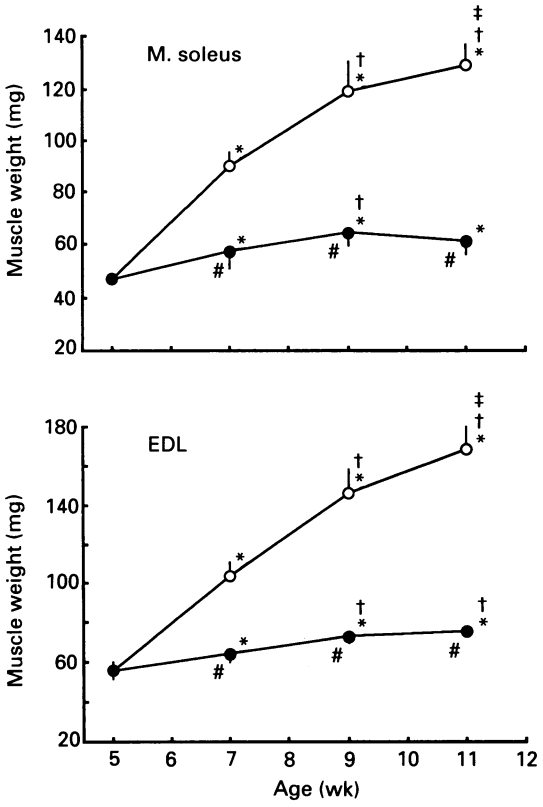

Fig. 1. Changes in muscle weights of soleus and EDL with age in groups 1 (○) and 2 (●). Values are means ± S.D. * Different from 5-wk-old rats ($P < 0.05$); † different from 7-wk-olds ($P < 0.05$); ‡ different from 9-wk-olds ($P < 0.05$); # different from group 1 ($P < 0.05$).

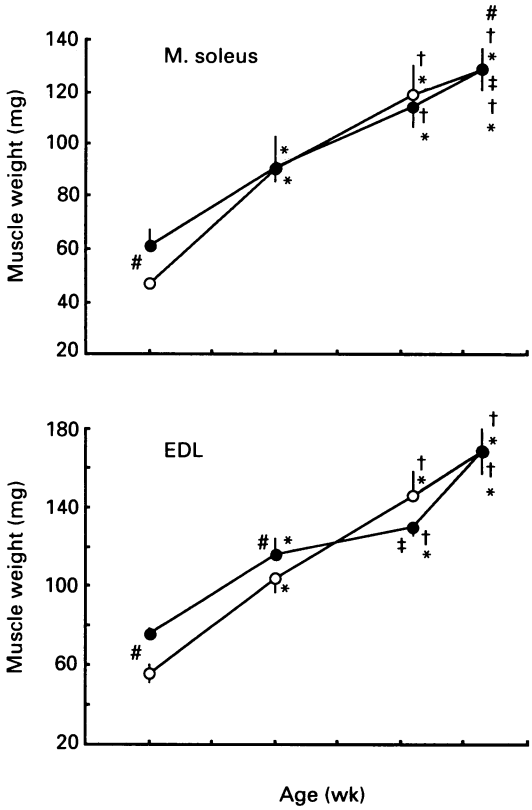

Fig. 2. Changes in muscle weights of soleus and EDL with increasing body weight in groups 1 (○) and 3 (●). Values are means ± S.D. * Different from 150 g body weight ($P < 0.05$); † different from 250 g body weight ($P < 0.05$); ‡ different from 360 g body weight ($P < 0.05$); # different from group 1 ($P < 0.05$).

increasing body weight in groups 1 and 3 are shown in Figure 2. Muscle weights of soleus and EDL in groups 1 and 3 increased significantly with increasing body weight. Muscle weights for soleus and EDL at 150 g body weight in group 3 were significantly greater than those in group 1 ($P < 0.05$). The EDL at 250 g in group 3 was also heavier than for group 1 ($P < 0.05$), but the EDL at 360 g was less than for group 1 ($P < 0.05$).

Figure 3 shows changes in muscle fibre areas for soleus with age in groups 1 and 2. Muscle fibre areas for soleus increased significantly with age in groups 1 and 2. Both types I and IIA fibre areas of soleus at 7, 9 and 11-wk-old rats in group 2 were significantly less than those in group 1 ($P < 0.05$).

Changes in muscle fibre areas of soleus with increasing body weight in groups 1 and 3 are given in Figure 4. Both types I and IIA fibre areas of soleus in groups 1 and 3 increased significantly with increasing body weight.

Figure 5 shows changes in muscle fibre areas for EDL with age in groups 1 and 2. Muscle fibre areas for EDL increased significantly with age in groups 1

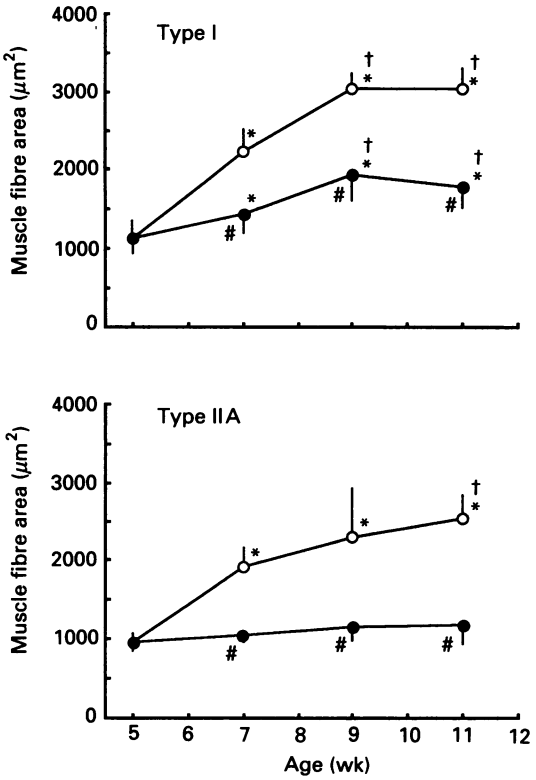

Fig. 3. Changes in muscle fibre areas in soleus with age in groups 1 (○) and 2 (●). Values are means ± S.D. For further explanation, see Figure 1.

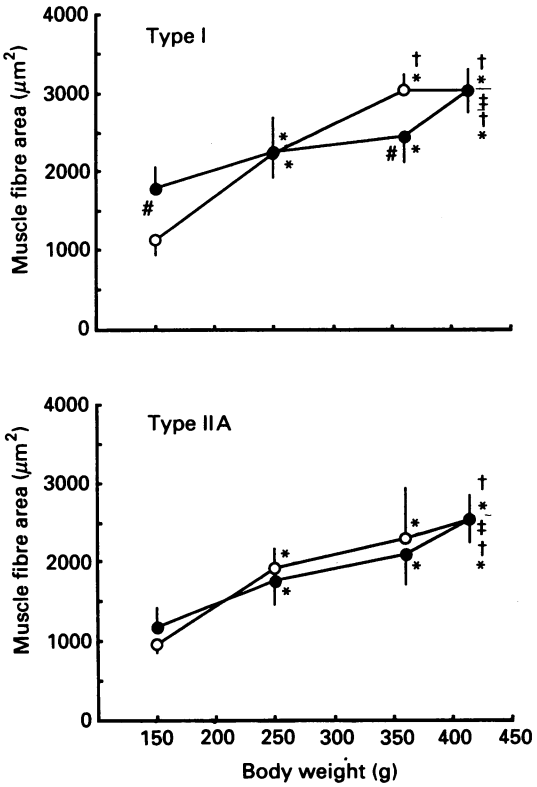

Fig. 4. Changes in muscle fibre areas in soleus with increasing body weight in groups 1 (○) and 3 (●). Values are means ± S.D. For further explanation, see Figure 2.

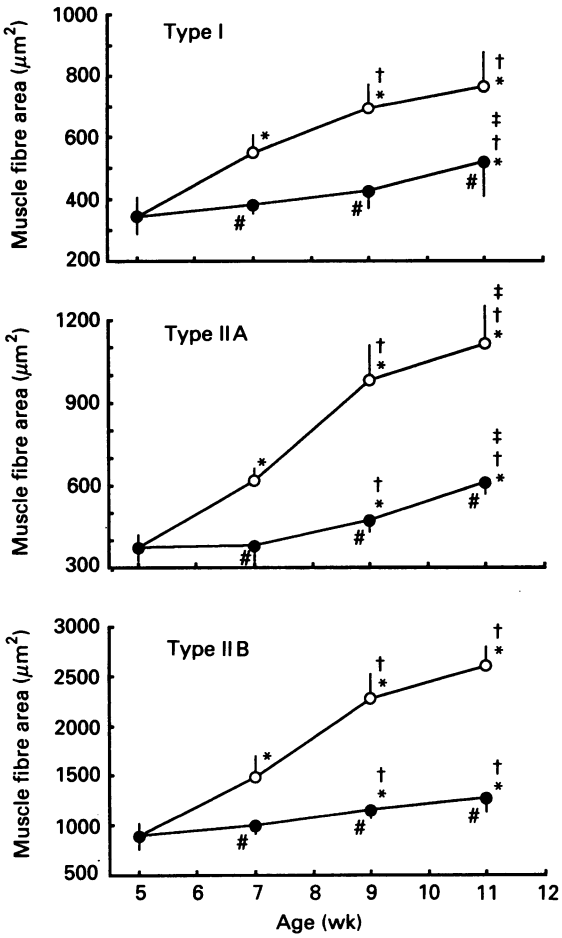

Fig. 5. Changes in muscle fibre areas in EDL with age in groups 1 (○) and 2 (●). Values are means ± S.D. For further explanation, see Figure 1.

and 2. Type I, IIA and IIB fibre areas of EDL in 7, 9 and 11-wk-old rats in group 2 were significantly smaller than those in group 1 ($P < 0.05$).

Changes in muscle fibre areas of EDL with increasing body weight in groups 1 and 3 are shown in Figure 6. Types I, IIA and IIB fibre areas for EDL in groups 1 and 3 increased significantly with increasing body weight. Each of the fibre types at 150 g body weight and type IIA and IIB fibres at 250 g body weight in group 3 were significantly larger than those in group 1 ($P < 0.05$).

Muscle fibre types

Changes in the percentage of muscle fibre types for soleus with age in groups 1 and 2 are shown in Figure 7. There were significant increases ($P < 0.05$) in the percentage of type I fibres with age in groups 1 and 2, whereas the opposite changes ($P < 0.05$) occurred for the percentage of type IIA fibres.

Figure 8 shows changes in the percentage of muscle

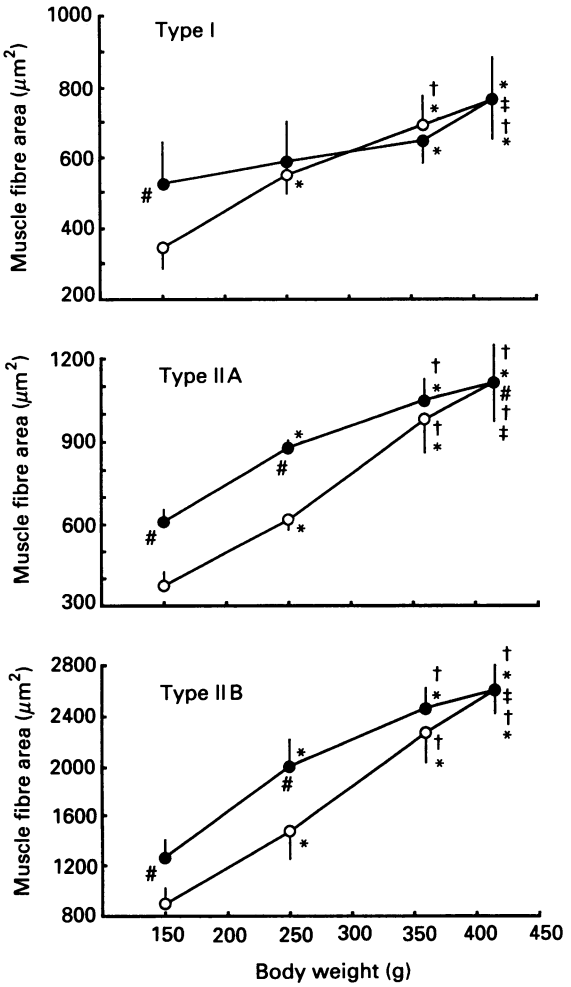

Fig. 6. Changes in muscle fibre areas in EDL with increasing body weight in groups 1 (○) and 3 (●). Values are means±S.D. For further explanation, see Figure 2.

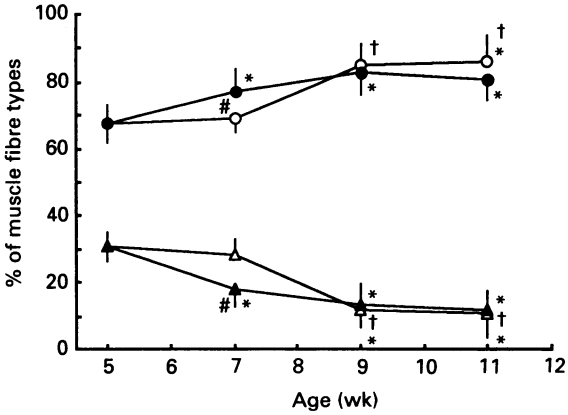

Fig. 7. Changes in the percentage of muscle fibre types in soleus with age in groups 1 and 2. Values are means±S.D. For further explanations, see Figure 1. ○, Type I in group 1; ●, type I in group 2; △, type IIA in group 1; ▲, type IIA in group 2.

fibre types for soleus with increasing body weight in groups 1 and 3. In group 1 there was a significant increase in the percentage of type I fibres ($P < 0.05$)

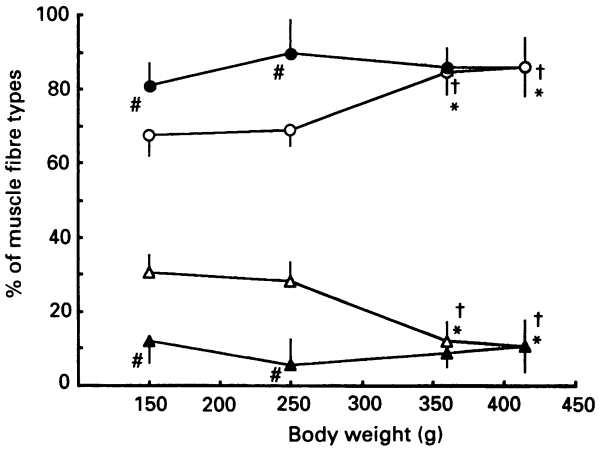

Fig. 8. Changes in muscle fibre types in soleus with increasing body weight in groups 1 and 3. Values are means±S.D. For further explanation, see Figure 2. ○, Type I in group 1; ●, type I in group 3; △, type IIA in group 1; ▲, type IIA in group 3.

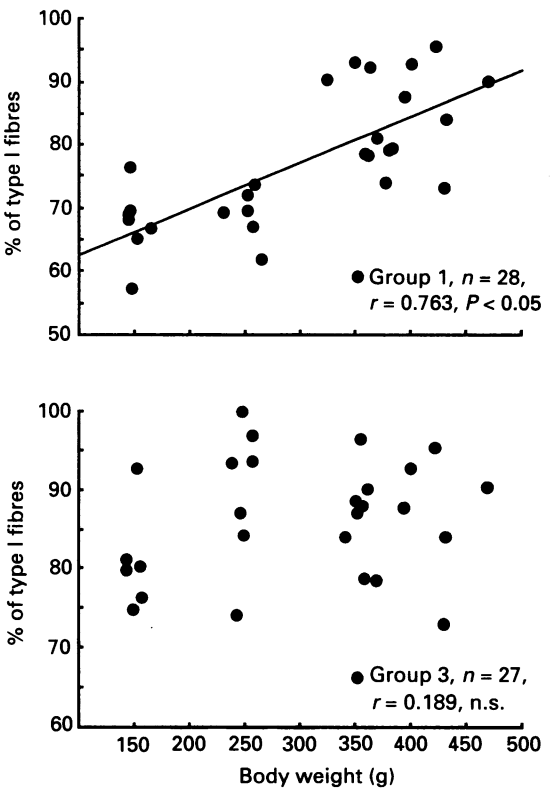

Fig. 9. Relationships between the percentage of type I fibres in soleus and body weight in groups 1 and 3.

and a decrease in the percentage of type IIA fibres ($P < 0.05$), but no change in group 3. Figure 9 shows relationships between the percentage of type I fibres of soleus and body weight in groups 1 and 3. There was a significant correlation ($r = 0.763$, $P < 0.05$) between the percentage of type I fibres and body weight in group 1, but not in group 3 ($r = 0.189$, n.s.).

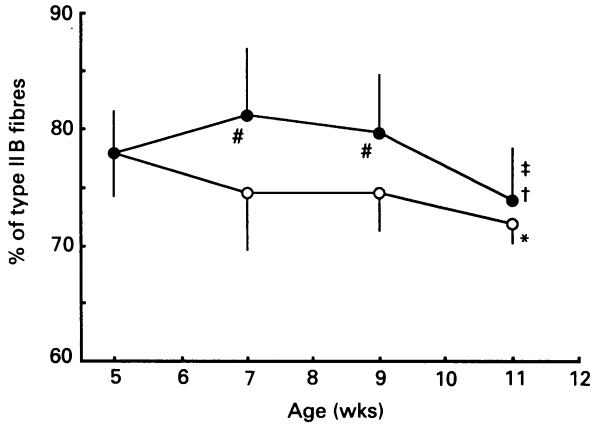

Fig. 10. Changes in the percentage of type IIB fibres in EDL with age in groups 1 (○) and 2 (●). Values are means ± S.D. For further explanation, see Figure 1.

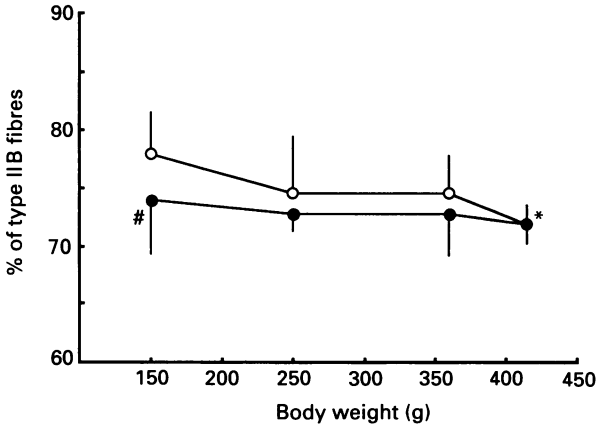

Fig. 11. Changes in the percentage of type IIB fibres in EDL with increasing body weight in groups 1 (○) and 3 (●). Values are means ± S.D. For further explanation, see Figure 2.

Figure 10 shows changes in the percentage of type IIB fibres for EDL in groups 1 and 2. In group 1 the percentage of type IIB fibres for 11-wk-old rats was significantly less that that at 5 wk ($P < 0.05$). In group 2 there was no difference between the percentage of type IIB fibres for 5 and 11-wk-old rats, but the percentage of type IIB fibres for 11-wk-old rats was significantly less than that at 7 and 9 wk.

In group 1, the percentage of type IIB fibres for EDL decreased significantly with increasing body weight ($P < 0.05$), but the percentage did not change in group 3 (Fig. 11). The percentage of type IIB fibres at 150 g body weight in group 3 was significantly less than that at 150 g in group 1 ($P < 0.05$). Figure 12 shows the relationships between the percentage of type IIB fibres for EDL and body weight in groups 1 and 3. There was a significant correlation ($r = -0.498$, $P < 0.05$) between the percentage of type IIB fibres and body weight in group 1, but not in group 3 ($r = -0.210$, n.s.).

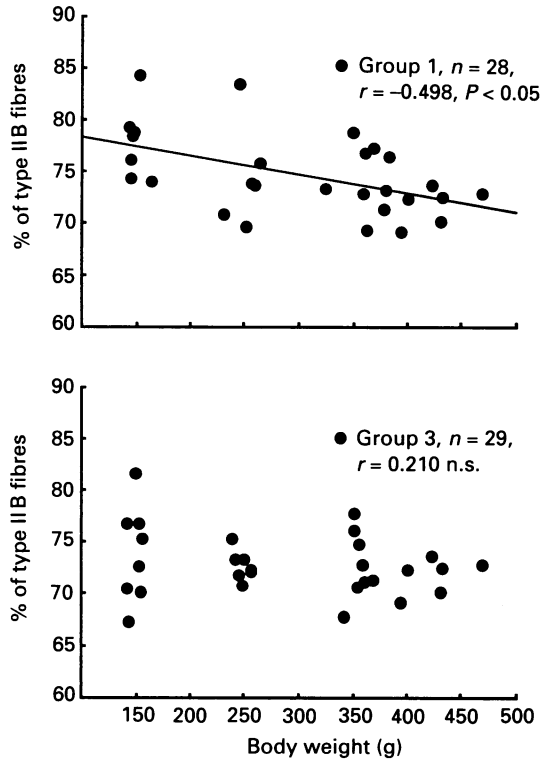

Fig. 12. Relationships between the percentage of type IIB fibres in EDL and body weight in groups 1 and 3.

DISCUSSION

This study has shown that muscle weights and fibre areas are strongly influenced by increasing body weight. These results are similar to previous studies that reported a close correlation between body weight and muscle weight or fibre areas (Sillau & Banchero, 1977; Ripoll et al. 1979; Tamaki, 1985; Smith et al. 1989). These results suggest that the increases of muscle weight and fibre areas with age can be related to the increasing body weight. In this study, the decrease of body weight was achieved through food restriction. It is not possible to separate the effects of body weight from other consequences of food restriction, such as hormonal or activity changes.

Despite the fact that body weight in each of the subgroups in group 2 was identical, muscle weight and fibre areas increased significantly with age. The older rats in group 2 were subjected to more severe food restriction. In general, severer food restriction will make the muscle weights and fibre areas smaller. However, in this study the rats had larger muscle weights and fibre areas. It would suggest that the factors associated with food restriction were not related to the increases of muscle weight and fibre areas with age in group 2. A possible explanation is the rapidity of increasing body weight in freely fed rats. The changes of muscle weight and fibre areas are

mainly influenced by the magnitude of the imposed muscle overload. The increases of muscle weight and fibre areas in freely fed rats may not have caught up with the increasing body weight. As body weight in the rats with reduced food intake increased more slowly with age, it could make muscle weight and fibre areas larger. Another possibility is that the difference in muscle weights may be related to muscle length. Even though body weight is the same, older rats may have greater muscle lengths. Unfortunately, as muscle lengths were not measured in this study, we are unable to estimate their effects.

We attempted to investigate whether the retardation in the increase of body weight by reduced food intake could change the transformation of muscle fibre types with growth. Although in group 3 the heaviest rats weighed about three times as much as the lightest, the distribution of muscle fibre types of soleus and EDL was the same. In addition, the correlations between muscle fibre types and body weight observed in group 1 did not emerge in group 3 of the same age. Furthermore, the muscle fibre types for soleus and EDL in group 2 of the same body weight changed with age. It seems that the increase in body weight is not related to the transformation of muscle fibre types with growth. These results contradict the reports that indicate a direct relationship between the proportion of type I fibres of soleus and body weight (Sillau & Banchero, 1977; Ripoll et al. 1979; Aquin et al. 1980; Tamaki, 1985). Unlike the present study, these reports did not distinguish increasing body weight from age. Thus if the relationship between increasing body weight and transformation of muscle fibre types with growth is only judged from such studies, the relationship would be misunderstood.

As the present study changed body weight by reducing food intake, it is possible that the reduced food intake influenced muscle fibre composition. However, in group 3 differences in muscle fibre types between each of the subgroups were not observed. Thus in this study reduced food intake may not have been important for the transformation of muscle fibre types with growth. This notion would be in line with the results of Goldspink & Ward (1979) and Boreham et al. (1988).

What factors cause the transformation of muscle fibre types after 5 wk? One possibility may be the increase in activity in growing rats. Ishihara et al. (1991) reported that exercising rats possessed a higher percentage of FOG fibres in plantaris than control rats. In addition, Wernig et al. (1990) showed that exercising rats had a higher proportion of type I fibres in skeletal muscles. However, as there was insufficient cage space for the rats to exercise in this study, voluntary exercise would be unlikely to be related to the transformation of muscle fibre types.

Another possibility is the effect of testosterone. It has been reported that testosterone may alter the distribution of muscle fibre types (Vaughan et al. 1974; Kelly et al. 1985; Holmäng et al. 1990). However, there were no sexual differences on muscle fibre composition in rats (Sugiura et al. 1986). In addition, testosterone would increase the percentage of type II fibres at the expense of type I fibres (Vaughan et al. 1974; Kelly et al. 1985; Holmäng et al. 1990). As transformation of muscle fibre types with growth was opposite to the effect of testosterone, it is unlikely that it is related to testosterone.

A further possibility is that other hormones, such as thyroid or growth hormones, may be related to the transformation of muscle fibre types between 5 and 11-wk-old rats. Although it has been reported that the transformation of muscle fibre types is related to growth hormone (Ayling et al. 1989) and thyroid hormone levels (Ianuzzo et al. 1977; Nwoye et al. 1982; Izumo et al. 1986), the relationship between these hormones and the transformation between 5 and 11 wk remains unclear.

Finally, it is suggested that the transformation of muscle fibre types between 5 and 11-wk-old rats is not influenced by factors associated with food restriction. These observations may indicate that investigations into muscle fibre composition during growth should consider the age of the animals rather than their body weight.

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