# A2. THE STRESS SYNDROME AND MEAT QUALITY

## THE EFFECT OF BODY SIZE AND SELECTION ON SKELETAL MUSCLE FIBRE TYPES IN MAMMALS

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This study attempts to define and resolve some of the histochemical variations in the muscle fibres of mammals, and to demonstrate how the histochemical properties of muscle fibres may be influenced by selection and growth.

Fibre type profiles have been established in the diaphragm and M. semitendinosus of mammals of different body size, using succinate dehydrogenase as an indicator of aerobic capacity, phosphorylase as an indicator of anaerobic capacity and myosin adenosine triphosphatase as an indicator of intrinsic speed of contraction of individual fibres - fibres having a high activity of this enzyme being fast-twitch and those having a low activity being slow-twitch.

By using transverse frozen serial sections and back projection, histochemical profiles of about 400 individual muscle fibres were made on each sample taken from the diaphragms of adult shrews, mice, rats, rabbits, cats, dogs, sheep, pigs, oxen and horses; and from the semitendinosus muscle of adult mice, rats, rabbits, cats, dogs and horses. From these profiles the following types of muscle fibres were found: fast-contracting, aerobic; fast-contracting, with both aerobic and anaerobic capacity; fast-contracting, anaerobic; slow-contracting, aerobic; and slow-contracting, with both aerobic and anaerobic capacity. The proportion of slow-twitch fibres in the diaphragm and M. semitendinosus increases with increasing body size. This finding corresponds to a decreasing speed of movement of the diaphragm and limbs with increasing body size.

An increase in the proportion of fibres that are low in myosin adenosine triphosphatase activity, was seen in the longissimus muscles from 34 Large White pigs ranging from 1·3 to 93 kg live weight. This finding indicates a modification in the properties of some muscle fibres during growth to enable the animal to support itself.

A study of M. semitendinosus and M. anterior pectoral in 10 Thoroughbreds and 9 other horses, 33 Greyhounds and 9 other dogs, all the animals used being adults, showed that the Thoroughbreds and Greyhounds - breeds which have been selected to run quickly, had a lower proportion of slow-twitch fibres, in relation to their body size, than animals from other breeds.

## L'EFFET DE LA TAILLE DU CORPS ET DE LA SELECTION SUR LE MUSCLE SQUELETTIQE TYPES DE FIBRES CHEZ LES MAMMIFERES

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Cette étude tente de définir et de résoudre certaines variations histochimiques dans les fibres musculaires des mammifères et de demonstrer comment les propriétés histo-chimiques des fibres musculaires peuvent etre influencées par la sélection et la croissance.

Des profils de type fibreux ont été établis dans le diaphragne et les muscles semi-tendineux de mammifères de taille differente, en utilisant la succinate deshydrase comme indicateur de la capacité aérobie, la phosphorylase comme indicateur de la capacité anaérobie et l'adénosine triphosphatase de myosine comme indicateur de vitesse de contraction intrinséque des fibres individuelles - les fibres réagissant beaucoup à cette enzymetétant à contraction rapide et celles réagissant moins étant à contraction lente.

En utilisant des sections transversales gelées et la "Back Projection", des profils histo-chimiques d'environ 400 fibres de muscle individuelles furent faits de chaque échantillon pris sur les diaphragmes de musaraignes adultes, souris, rats, lapins, chats, chiens, porcs, moutons, boeufs et chevaux: et du muscle semi-tendineux de souris, rats, lapins, chats, chiens et chevaux adultes. A partir de ces profils, on a découvert les différents types de fibres musculaires suivants: contraction rapide, aérobie; contraction rapide avec a la fois une capacité aérobie et anaerobie; contraction rapide anaérobie; contraction lente, aérobie; et contraction lente avec à la fois avec une capacité aérobie et capacité anaérobie. La proportion des fibres a contraction lente dans le diaphragme et les muscles semi-tendineux augmente avec l'accroissement de la taille. Cette découverte correspond à un ralentissement de la vitesse du movement due diaphragme et des membres avec l'accroissement de la taille du corps.

On a observé chez 34 porcs de type White Large (Blanc gros) dont le poids (vivant) varie de 1·3 kg. a 93 kg., un accroissement dans la proportion des fibres des muscles les plus longs qui ont une activité basse en triphosphatase adénosine de myosine. Cette découverte indique une modification des propriétés de certaines fibres musculaires pendant la croissance, en vue de permettre à l'animal de supporter son propre poids.

Une étude des muscles semi-tendineux et des muscles pectoraux antérieurs de 10 chevaux de race pure et de 9 autres chevaux, de 33 lévriers et de 9 autres chiens (tous ces animaux étant adultes) a montré que les chevaux de race pure et les lévriers - races qui ont été sélectionnées pour courir vite - ont une proportion de fibres musculaires à contraction lente plus basse par rapport à la taille de leur corps, que les animaux d'autres races.

## AUSWIRKUNG VON KÖRPERGRÖSSE UND ZUCHTWAHL AUF SKELETTMUSKELFASERTYPEN BEI SÄUGETIEREN

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Zweck dieser Studie sind Definition und Analyse einiger histochemischer Variationen in Muskelfasern von Säugetieren. Es soll gezeigt werden, wie die histochemischen Eigenschaften von Muskelfasern durch Zuchtwahl und Wachstum beeinflußt werden können.

Im Diaphragma und M. semitendinosus von Säugetieren verschiedener Körpergröße wurden Fasertypprofile erstellt, unter Verwendung von Succinatdehydrogenase als Indikator aerober Kapazität, Phosphorylase als Indikator anaerober Kapazität und Myosin-Adenosin-Triphosphatase als Indikator der inhärenten Kontraktionsgeschwindigkeiten einzelner Fasern. (Fasern mit hoher Aktivität dieses Enzyms haben hohe, Fasern mit geringer Aktivität geringe Kontraktionsgeschwindigkeit.)

Unter Verwendung tiefgekühlter transversaler Serienschnitte und Durchprojektion wurden histochemische Profile von ungefähr 400 einzelnen Muskelfasern aus jeder Probe erstellt, die dem Diaphragma ausgesachsener Spitzmäuse, Mäuse, Ratten, Kaninchen, Katzen, Hunden, Schafen, Schweinen, Ochsen und Pferden sowie dem M. semitendinosus ausgewachsener Mäuse, Ratten, Kaninchen, Katzen, Hunden und Pferden entnommen waren. Aus diesen Profilen ließen sich folgende Typen von Muskelfasern bestimmen: schnell kontrahierend, aerob; schnell kontrahierend, aerob und anaerob; schnell kontrahierend, anaerob; langsam kontrahierend, aerob; langsam kontrahierend, aerob und anaeob. Der Anteil von Fasern mit langsamer Kontraktion im Diaphragma und M. semitendinosus nimmt mit zunehmender Körpergröße zu. Dieser Befund entspricht der verringerten Geschwindigkeit der Bewegung in Diaphragma und Gliedern bei zunehmender Körpergröße.

Ein zunehmender Anteil von Fasern mit geringer Myosin-Adenosin-Triphosphatase-Aktivität wurde im M. longissimus von 34 Großen Weißen Schweinen mit einem Lebendgewicht von 1·3 kg - 93 kg gefunden. Dieser Befund weist auf eine Veränderung der Eigenschaften einiger Muskelfasern während des Wachstums zur Gewährleistung der Standfestigkeit des Tiers hin.

Eine Studie des M. semitendinosus und M. anterior pectoral bei 10 Vollblut- und 9 anderen Pferden, 33 Windhunden und 9 anderen Hunden (durchwegs ausgewachsene Tiere) zeigte, daß die Vollblutpferde und die Windhunde, die für schnelles Laufen gezüchtet werden, einen geringeren Anteil von Fasern mit langsamer Kontraktion bezogen auf die Korpergroße aufwiesen als Tiere anderer Züchtungen.

## ВЛИЯНИЕ РАЗМЕРА ТЕЛА И СЕЛЕКЦИИ НА ТИПЫ СКЕЛЕТНЫХ МЫШЕЧНЫХ ТКАНЕЙ МЛЕКОПИТАЮЩИХ.

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Это исследование пытается определить некоторые гистохимические отклонения в мышечных тканей млекопитающих, и показать, как могут влиять на гистохимию мышечных тканей процессы селекции и роста.

Установили профиля типов тканей в диафрагме и в полусухожильной мышце млекопитающих разных размеров, используя сукцино-дегидразу как указатель аэробной способности, фосфорилазу как указатель анаэробной способности и миозинаденозинтрифосфатазу как указатель присущей сократительной скорости отдельных тканей; причем, ткани, отличающиеся высокой активностью этого энзима - быстро-сокращающиеся, а ткани, имеющие низкую активность этого энзима - медленно-сокращающиеся.

Методом проекции поперечных замороженных серийных разрезов установили профиля примерно 400 отдельных мышечных тканей на каждой пробе, полученной из диафрагм взрослых землероек, мышей, крыс, кроликов, кошок, собак, овец, свиней, волов и лошадей; и из полусухожильных мышец взрослых мышей, крыс, кроликов, кошок, собак и лошадей. Изучая эти профиля, нашли следующие типы мышечных тканей: быстро-сокращающиеся, аэробные ткани, быстро-сокращающиеся с аэробной и анаэробной способностью быстро-сокращающиеся, анаэробные; медленно-сокращающиеся, аэробные, и медленно-сокращающиеся, как и с аэробной, так и с анаэробной способностью. Число тканей в диафрагме и в полусухожильной мышце, сокращающиеся медленно, увеличивается соразмерно размеру тела; этот вывод соответствует уменьшению скорости движения диафрагмы и членов по мере увеличения размера тела.

В длинных мышцах от 34 больших белых свиней, в пределах от 1,3 до 93 кг живого веса, обнаружили увеличение количества тканей, в которых миозинаденозинтрифосфатаза малоактивна. Это указывает на то, что в процессе роста, вещества некоторых мышечных тканей изменяются, чтобы животное могло стоять.

Изучение полусухожильной мышцы и передней грудной мышцы на 10 чистокровных и на 9 других лошадях, на 33 борзых и на 9 других собаках ( причем все изучаемые животные были взрослые) показало, что в чистокровных и борзых - породах, выбранных для быстрого бега - количество медленно-сокращающихся тканей по сравнению с размером тела меньше, чем у животных других пород.

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### INTRODUCTION

Systems of classification of muscle fibres based on histochemical reactions have largely ignored the functional significance of the methods used. Nomenclature of fibres has been in terms of colour descriptions (Ogata, 1958), numerals (Dubowitz & Pearse, 1960; Engel, 1962) and alphabetical symbols (Stein & Padykula, 1962; Guth, Samaha & Albers, 1970; Brooke & Kaiser, 1970; Ashmore & Doerr, 1971), based on observations of histochemical reactions in muscle fibres of numerous muscles in a variety of mammals. These systems of classification may be superseded if fibres can be characterised by their mechanical and metabolic properties.

In this study the use of selected histochemical reactions and profile construction has enabled classification of individual fibres to be made according to their intrinsic speed of contraction and their capacity for aerobic and anaerobic metabolism. The myosin adenosine triphosphatase (myosin ATPase) reaction is used to indicate the intrinsic speed of contraction of a fibre - fibres having a high activity of this enzyme being fast-twitch those having a low activity being slow-twitch (Burke, Levine, Tsairis & Zajac, 1973). Succinate dehydrogenase activity is used as an indicator of aerobic metabolism and glycogen phosphorylase as an indicator of anaerobic metabolism. The diaphragm was used to establish histochemical profiles in a variety of mammals because it has a similar function in all the animals studied.

An increase in the proportion of fibres that are low in myosin ATPase activity during postnatal growth has been reported in the pectineus muscle of the dog by Cardinet, Wallace, Fedde, Guffy & Bardens (1969). A similar observation has been made by Karpati & Engel (1967) on the soleus of the rat, guinea-pig and cat. To investigate this phenomenon it was decided to study the effect of increasing body weight on the histochemical characteristics of muscle fibres in the domestic pig, both because the extent of postnatal growth of the pig exceeds that of most other domestic animals, and the skeletal muscle of the pig appears to be unique in its organisation of histochemical fibre types in that one or more bundles of fibres characterised by low activity of myosin ATPase are located within perimysium enclosed fasciculi.

The members of the Thoroughbred breed of horse and Greyhound breed of dog are notably quicker runners than their fellow specific members. These breeds have been selected to run quickly for approximately 300 years in the case of the Thoroughbred and 3,000 years in the case of the Greyhound. The possibility that a selection procedure (the criterion of selection being speed of running) may influence the proportions of different types of fibres in the muscles of these breeds is investigated. The results have been reported previously by Davies & Gunn, 1971; Gunn & Davies, 1971; Davies & Gunn, 1972; Davies, 1972 and Gunn, 1973.

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### MATERIALS AND METHODS

Samples were taken from the costal diaphragm of adult shrews, mice, rats, rabbits, cats, dogs, pigs, sheep, cattle and horses; from the dorsomedial region of m. longissimus at the level of the thoraco-lumbar junction from Large White pigs of 1·3 to 93 kg. live weight; and from the left m. pectoralis transversus of horses at the manubrium sterni. The samples were removed from each animal within 45 minutes of death. Complete cross-sections of the middle third of m. semitendinosus from mice, rats, rabbits, cats, dogs and horses were also taken as soon as possible after death. The outline of the transverse sectional area (T.S.A.) of m. longissimus of pigs at the level of the thoraco-lumbar junction, adjacent to the sampling site, was drawn on paper and the T.S.A. measured by the paper weighing method.

After rapid freezing of a block of fresh muscle, about ten adjacent serial sections, 10 μm thick, were cut transversely to the direction of the muscle fibres. The histochemical methods used are described by Davies & Gunn (1972): they are modifications of the methods used by Nachlas, Tsou, de Souza, Cheng & Seligman (1957) to demonstrate succinate dehydrogenase activity; Takeuchi & Kuriaki (1955) to demonstrate glycogen phosphorylase activity; and Padykula & Herman (1955) to demonstrate myosin ATPase activity. The serial sections were back projected on to tracing paper so that individual fibres could be outlined and their metabolic profiles constructed. To estimate the level of activity of enzymes that showed a continuous spectrum of activity between fibres, a simple division into high and low was made for each fibre relative to the overall level of activity of fibres in each section. Mean fibre T.S.A. were estimated by counting the number of fibres projected within an area of known magnification and where applicable the mean T.S.A. of each fibre type was determined by cutting out and weighing the tracing paper on which the profiles were constructed.

Low power projection of sections stained for myosin ATPase activity enabled an assessment to be made of the number of myosin ATPase low reacting bundles of fibres in samples from m. longissimus of pigs. Using the measurement of the T.S.A. of the whole muscle, an estimate of the total numbers of bundles in the T.S.A. was made. At the same time, the number of myosin ATPase low fibres in each bundle was recorded and the mean number calculated. Similarly, the total number of myosin ATPase low reacting fibres was assessed in the m. semitendinosus of dogs by sampling the muscle at 2 mm. intervals across its entire transverse section. The total area of myosin ATPase low reacting fibres was calculated from this figure, and the mean area of myosin ATPase low reacting fibres in the section.

### RESULTS

The following types of fibres exist in significant though differing proportions, in the diaphragms of the ten species examined: fast-twitch, aerobic; fast-twitch, with both aerobic and anaerobic capacity; fast-twitch anaerobic; slow-twitch aerobic; and slow-twitch with both aerobic and anaerobic capacity. The proportions of each of these fibre types in the diaphragms of the ten species examined is given in Table 1.

Table 1 Percentages of histochemical fibre types in the diaphragm of ten mammalian species.

| Species | No. of animals studied | No. of fibres counted | Percentage of fibre types* | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Ah | | | | Al | | | | | | |
| | | | Sh | | Sl | | Sh | | Sl | | | | |
| | | | Ph | Pl | Ph | Pl | Ph | Pl | Ph | Pl | Ah | Sh | Ph |
| Shrew | 2 | 1120 | - | 100 | - | - | - | - | - | - | 100 | 100 | - |
| Mouse | 4 | 1436 | - | 93 | - | - | - | 7 | - | - | 93 | 100 | - |
| Rat | 3 | 1337 | 7 | 25 | 27 | 2 | 1 | 38 | - | - | 61 | 71 | 35 |
| Rabbit | 3 | 1605 | 21 | 4 | 36 | - | - | 43 | - | - | 57 | 64 | 57 |
| Cat | 2 | 1612 | 16 | - | 45 | - | - | 39 | - | - | 61 | 55 | 61 |
| Dog | 4 | 3573 | 64 | - | - | - | - | 36 | - | - | 64 | 100 | 64 |
| Sheep | 3 | 2938 | 43 | - | - | - | 43 | 14 | - | - | 43 | 100 | 86 |
| Pig | 6 | 2548 | 17 | 3 | 32 | 3 | 4 | 41 | - | - | 55 | 65 | 53 |
| Ox | 3 | 1879 | 24 | - | - | - | 58 | 18 | - | - | 24 | 100 | 82 |
| Horse | 2 | 2559 | 21 | - | - | - | 77 | 2 | - | - | 21 | 100 | 98 |

*Key: Ah, Sh, Ph: high activity of myosin ATPase, SDHase or phosphorylase respectively.
Al, Sl, Pl: low enzyme activity.

Table 1 demonstrates that the proportion of myosin ATPase high reacting (fast-contracting) fibres increased with decreasing body size. Differences in succinate dehydrogenase activity between fibres were not as conspicuous as the difference in myosin ATPase activity, and the porportion of fibres having a high or low succinate dehydrogenase activity did not show a body size correlation. Phosphorylase activity tended to show an opposite trend to that of myosin ATPase activity. The horse had nearly 100% of its fibres high in phosphorylase activity, but in the shrew diaphragm no fibres with high phosphorylase activity were seen.

In the larger species, fast contracting fibres were high in phosphorylase activity, showing that fast-contracting fibres in these species use mainly an anaerobic metabolism. In smaller animals, however, the proportion of fibres with high myosin ATPase activity exceeded that of fibres with high phosphorylase activity, demonstrating that fast-contracting fibres may also use aerobic metabolism.

Observations on the complete cross sections of m. semitendinosus of mice, rats, rabbits, cats, dogs and horses of mixed breeds, showed that the caudal superficial region of the muscle of smaller animals contained only myosin ATPase high reacting fibres. With increasing body size, the deep region of mixed fibre population occupied a larger proportion of the muscle and the proportion of its fibres low in myosin ATPase activity increased.

The transverse sectional area of m. longissimus of the pigs studied, increased with increasing body weight in a relationship to the $^2/_3$ power of the body weight. The increase in mean fibre transverse sectional area is directly proportional to the transverse sectional area of the whole muscle in pigs of live weight from 3·7 to 98 kg. The histological appearance of the endomysium and perimysium did not suggest a disproportionate development of tissues other than muscle fibres. After ten days of age (3·7 kg live weight in this study), growth in T.S.A. of m. longissimus of the pig is therefore accounted for by growth of a constant population of muscle fibres.

The number of myosin ATPase low reacting bundles of fibres remained constant throughout growth. However, the mean number of fibres per bundle increased from 1·0 in early postnatal life to 3·2 at 98 kg. live weight (Fig. 1).

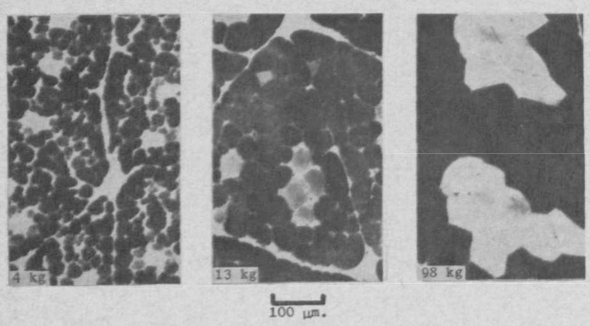


Fig. 1. Fibre types differentiated by the myosin ATPase reaction in m. longissimus at three stages of growth.

Fibres with intermediate reaction for myosin ATPase were seen adjacent to the "myosin ATPase low bundles". This observation was made frequently in pigs between birth and 15 kg. live weight.

Comparison of the T.S.A. of the muscle occupied by myosin ATPase low reacting fibres with total body weight by means of double logarithmic regressions showed that the area of the muscle occupied by myosin ATPase low reacting fibres bears a linear relationship to body weight ($\log Y = 0{\cdot}99 \times \log X$).

The results obtained by assessing the total area of m. semitendinosus occupied by slow-twitch fibres in 12 Greyhounds and eight other dogs are given in Table 11. The area occupied by slow twitch fibres in the Greyhound is significantly less than the other dogs at the ·1% level. In samples from similar areas of m. pectorales transversus of five Thoroughbreds and six other horses, the area of slow-twitch fibres was significantly less at the ·5% level in Thoroughbreds than in other horses.

Table 11

QUANTITATIVE HISTOCHEMISTRY OF THE CANINE SEMITENDINOSUS MUSCLE

Proportion of the transverse sectional area occupied by myosin ATPase low reacting (slow-twitch) fibres

| GREYHOUNDS | | | | OTHER DOGS | | | | |
|---|---|---|---|---|---|---|---|---|
| Dog No. | Sex | Body Weight (kg) | % | Dog No. | Breed | Sex | Body Weight (kg) | % |
| 1 | ♂ | 37 | 3·3 | 1 | Great Dane | ♂ | 47 | 5·4 |
| 2 | ♂ | 26 | 1·6 | 2 | Collie | ♂ | 14 | 12·8 |
| 3 | ♂ | 29 | 0·8 | 3 | Collie | ♀ | 12 | 26·6 |
| 4 | ♂ | 27 | 3·2 | 4 | Collie | ♀ | 22 | 10·2 |
| 5 | ♂ | 31 | 2·8 | 5 | Labrador | ♀ | 33 | 14·9 |
| 6 | ♂ | 34 | 3·3 | 6 | Terrier X | ♀ | 10 | 14·2 |
| 7 | ♂ | 25 | 3·3 | 7 | Afghan | ♀ | 25 | 11·0 |
| 8 | ♂ | 31 | 5·1 | 8 | Afghan | ♂ | 32 | 7·0 |
| 9 | ♂ | 30 | 0·3 | | | | | |
| 10 | ♂ | 34 | 2·8 | | | | | |
| 11 | ♀ | 34 | 1·6 | | | | | |
| 12 | ♀ | 22 | 0·9 | | | | | |
| | | MEAN | 2·4 | | | | MEAN | 12·8 |
| | | S.D. | 1·4 | | | | S.D. | 6·5 |

DIFFERENCE BETWEEN MEANS IS SIGNIFICANT AT THE 0·1% LEVEL

## DISCUSSION

### The effect of body size on fibre types in adult animals

The biochemical studies of Bertalauffy & Estwick (1953), on a series of mice and rats, show that the capacity of the diaphragm for aerobic metabolism decreases with increasing body size. On that basis it may be expected that the capacity for oxidative metabolism may be less in the diaphragm of the larger animals in our series, in fact they have a high capacity for aerobic metabolism as shown histochemically, and also a capacity for anaerobic metabolism, presumably for brief periods of high respiratory rate.

The increasing proportion of fast-twitch fibres with decreasing body size may be related to the faster speed of contraction of the diaphragm in smaller mammals. The proportion of fast-twitch fibres in m. semitendinosus also appears to be inversely proportional to body size, although the effect is not as marked as in the diaphragm. This property of m. semitendinosus is to be expected from dimensional theory (Hill, 1950), according to which the limb muscles of larger animals should have a lower intrinsic speed of contraction.

The unequal distribution of slow-twitch fibres across the transverse section of m. semitendinosus results in a higher incidence of slow-twitch fibres in the deep, medial region than the superficial lateral region of the muscle. This allows the deep region to be more suited for a postural function, and the superficial region having a greater mechanical advantage to be more suited for a predominantly propulsive function.

### The effect of changing body size during growth on m. longissimus of pigs

If an animal maintains roughly the same shape as it grows, the cross-sectional area of any muscle will increase only by a factor of the 2/3 power of the weight. This was confirmed by the comparison, using double logarithmic regressions, of T.S.A. of m. longissimus with total body weight. Although the muscle should become proportionally weaker by this growth, the T.S.A. of the muscle occupied by slow-twitch fibres in fact increases in direct proportion to body weight. Awan & Goldspink (1972) have shown that slow-contracting fibres can develop and maintain more tension per µmole of creatine phosphate used and are therefore ergonomically more efficient for postural activity than fast-contracting fibres. Thus, the contractile apparatus of m. longissimus adapts to the changing demands placed on it during growth by the relative increase in more economical fibres. Histochemical evidence has been obtained which shows that this adaptation may cause a transformation of the physiological properties of certain fibres.

### The effect of selection for speed of running on fibre types

On a body size basis it might be expected that large horses and dogs should have a greater area of their skeletal muscle occupied by slow-contracting fibres than smaller members of their species. However, as Thoroughbreds and Greyhounds have a lower proportion of slow-contracting fibres in their limb muscles than smaller members of their species, a procedure of selection for rapid movement may override the effect of body size. So selection for speed has produced, over a large number of generations, animals with subtle differences in their musculature. These differences appear to be neurogenically determined since the myosin ATPase activity of a fibre is influenced by its type of innervation. Therefore, the differences seen in the proportion of different types of fibres in the muscles of these animals may be allied to differences in their nervous system.

### General Discussion

The ratio of slow-contracting to fast-contracting fibres, as determined histochemically, can be related functionally to ontogenetic and phylogenetic increase in size, to selection for rapid limb movement and to the functional demands made on different parts of the same muscle.

Changes in the characteristics of muscle fibres as basic as the ATPase activity of its myosin and its intrinsic speed of contraction imply considerable adjustment of the motor unit. During normal growth this change may involve either the conversion of a motor neurone, or a localized denervation of a muscle fibre associated with a colonizing re-innervation from a neighbouring motor unit of a different type. These possibilities merit further investigation.

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