J. Anat. (1975), **119**, 2, pp. 347–357
With 15 *figures*
Printed in Great Britain

Increase in fibre numbers of the rat pterygoid muscles during postnatal growth

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(*Accepted* 20 *October* 1974)

INTRODUCTION

MacCallum stated in 1898 that virtually all the fibres of the human sartorius muscle are formed before birth. This view has often been repeated, and it implies that postnatal growth of muscle depends on increase in girth and length of the individual fibres without any increase in their number. MacCallum did not investigate other muscles and, indeed, there do not appear to have been any similar studies on human muscles until Montgomery (1962) estimated the fibre numbers of the sartorius by a sampling method. He claimed there was a slight increase in the first postnatal year, and a smaller fibre population in the elderly.

MacCallum's statement about human muscle ought not to be extended to other species, because comparison of the newborn of different mammals shows that birth bears no fixed relationship to the stage of development attained in the animal generally and in the muscles in particular. Correlation between fibre population and ontogeny has therefore been studied in the pterygoid muscles of the rat, following a previous detailed study (Rayne & Crawford, 1971) of the development of these muscles. There are a few scattered discussions in the literature concerning fibre number (e.g. Goldspink, 1972), but the drawbacks of sampling methods are rarely mentioned. In view of this, a brief summary of previous work follows.

The best way of estimating fibre number is to choose a muscle in which a section can be cut through all the fibres, and then to count every fibre. There are few cases in which this has been done, and false conclusions may have arisen because the internal architecture had not been taken into account. In the case of pennate muscles, for instance, it may not be possible to select a cross section plane which will cut all the fibres, while some fusiform muscles, such as the human sartorius (Barrett, 1962), have their fibres arranged in series, so that any fibre count in a single transverse section should be multiplied by the number of series. The conclusions of both MacCallum and Montgomery which are mentioned above could be criticized for failing to make due allowance for these complications.

Riedel (1874) examined transverse sections of the sartorius muscle of the frog (which he claimed to be at the same stage of development as that of a mammal at birth) and, using a total fibre-counting method, found no increase in the number of fibres after this stage. Although the fibres may well run the length of the belly in this animal, the possibility of staggering was not taken into account. Morpurgo (1898) counted the number of muscle fibres in the M. radialis of five rats of different ages.

He claimed there was an increase from about 6000 at birth to 8000 in the fully grown. Stingl (1972) found a 20 % increase in the number of fibres in counts of transverse sections of a separate slip of spinotrapezius of the rat during the first week after birth. Enesco & Puddy (1964), however, found no increase in biceps brachii, extensor carpi, radialis longus, gastrocnemius or tibialis anterior in the rat from two weeks onwards. They claimed that they included all the fibres in the muscle by counting the total number in a cross section, but they do not seem to have considered the possibility, or significance, of some of the fibres being arranged in series. Moreover they only counted the fibres in the muscles of four sucklings and four adults. Goldspink (1962) reported an approximately eight fold increase in the fibre number of biceps brachii after birth in mice. However, using a total counting method, Rowe & Goldspink (1969) subsequently showed there was no increase in the fibre number of the tibialis anterior, biceps brachii, extensor digitorum longus, soleus and sternomastoid muscles of mice after birth. They pointed out that the discrepancy may have been due to the fact that only fully differentiated fibres were counted in Goldspink's earlier work, whereas the later study included the less differentiated fibres as well. This illustrates the importance of specifying the type of fibre counted when comparisons are made between the results of different workers. Bridge & Allbrook (1970) investigated the fibre number in two limb muscles of a marsupial, the quokka, during postnatal growth. The quokka is born very immature, the hind limb especially being merely a bud. Counts of the entire cross sectional areas showed a fourteen fold increase of fibre number of the extensor digitorum communis of the forelimb and a twenty nine fold increase in the case of the extensor hallucis et digiti secundi of the leg. These authors mention that the fibres of the former muscle run end to end throughout the belly, but do not comment on the architecture of the latter muscle.

Further information has been obtained by sampling methods. Staun (1963), ignoring muscle architecture and the proportion of cross sectional area occupied by non-fibre components, claimed there was no real change in fibre number in the longissimus dorsi and psoas muscles of the pig between the ages of 9 and 30 weeks: in fact there was a slight decrease in fibre number in older animals. Chiakulas & Pauly (1965) showed, by a sampling method, an increase in the fibre numbers of the muscles extensor carpi radialis longus (42 %) soleus (48 %) and plantaris (83 %) of the rat during the first three weeks of postnatal growth. A similar study of the cod has been made by Greer-Walker (1970). He assessed, by a sampling method which took into account the amount of connective tissue in the muscle, the total number of muscle fibres in the transverse section of the fish just cephalad to the most caudal dorsal fin. There is a relatively rapid increase in muscle fibre number up to a fish length of 40 cm. Then the rate of increase, although still exponential, is less, but continues throughout the growth in length of the fish.

The pterygoid muscles of the rat are small and as their fibres run the length of the muscle (Rayne, 1969), a cross section at its mid-point allows a reliable count of all the fibres to be made. The present study extends this preliminary work and sets out to count the total number of fibres in the medial and lateral pterygoid muscles of the rat during postnatal growth, and to relate changes in the size of the population to the histological appearances.

MATERIALS AND METHODS

Male and female Lister rats were used. Counts were made of the number of fibres in the medial and lateral pterygoid muscles of newborn, one week old, six week old and adult males and of six week old and adult medial pterygoid and adult lateral pterygoid muscles of females. The adults were fixed by perfusion with formol saline (NaCl 0·9 %, formaldehyde 4·0 %) and the heads of the young rats by immersion in the same fixative. Some heads were fixed in Fleming's mixture without acetic acid as recommended by Goldspink (1961), but it was found that the method of fixation did not affect the fibre counts. After 48 hours' fixation the muscles were dissected from the skull, great care being taken not to lose any of their fasciculi. Most of them were then placed in 10 % sulphuric acid for about 2 hours: this slightly separated the fibres and facilitated counting later. The muscles were dehydrated, cleared and embedded in paraffin wax, and serial transverse sections 8 μm thick were cut, stained with haematoxylin and eosin, and mounted in DPX. Photomicrographs were made of carefully chosen sections through the middle of the muscle belly. The fibres, including the immature myotubes of the day old muscles, were counted on enlarged prints, frequent reference to the original slide confirming accuracy in the identification of individual fibres and of the counts of specific areas.

A few muscles were embedded in gelatine, cut on a freezing microtome, mounted and stained with Sudan black, in order to compare our method with that of Hiiemäe (1966).

In order to investigate the cytology of the developing muscle, young rats were decapitated and the skin and superficial muscles were removed to expose the medial pterygoid and facilitate rapid penetration of the fixative into the muscles. The heads were usually immersed in Helly's fluid for about 24 hours, but sometimes other fixatives were used. Following fixation in Helly's fluid the muscles were dissected free from their attachments and postchromed in a saturated solution of potassium dichromate at 37 °C for 2–3 days. Then after 24 hours' washing in tap water they were dehydrated in ascending grades of ethanol and embedded in polyester wax at 38 °C. Sections 6 μm thick were cut and stained with iron haematoxylin.

OBSERVATIONS

Fibre numbers

The figures of the fibre counts of the medial pterygoid muscle are shown in Table 1 and of the lateral pterygoid muscle in Table 2. In the male, the number of fibres in the medial pterygoid muscle almost doubled in the first week after birth, and between the 1st and 6th weeks there was a further small but significant increase. Between the 6th week and the adult it was surprising to discover that there was a small but significant fall in fibre number. The number in the female was significantly less than in the male both at six weeks and in the adult and, as in the male, there was a decrease in the fibre number between six weeks and the adult stage.

In the lateral pterygoid muscle of the male the postnatal rate of increase of fibre numbers was less (Table 2). The figures show small non-significant increases between the succeeding stages, from newborn to one week, from one week to six weeks, and

Table 1. *The number of fibres in the medial pterygoid muscle during growth*

Sex	Age	Mean number of fibres per muscle	Standard error	Number of muscles	Student's '*t*' test *P*	Degrees of freedom
Male	Newborn	8,270	440	7	<0·001	12
	1 week	14,100	1,090	7	0·02–0·01	12
	6 weeks	17,540*	630	7	0·05–0·02	16
	Adult	15,560	520	9	0·01–0.002	16
Female	Adult	12,960	810	7	0·05–0·02	11
	6 weeks	15,100*	620	6		

* Number at six weeks in male greater than at six weeks in female. P = 0·02–0·01, with 11 degrees of freedom.

Table 2. *The number of fibres in the lateral pterygoid muscle during growth*

Sex	Age	Mean number of fibres per muscle	Standard error	Number of muscles	Student's '*t*' test *P*	Degrees of freedom
Male	Newborn	7,329*	368	14	>0·1	18
	1 week	8,250	694	6	0·1–0·05	9
	6 weeks	9,900	356	5	>0·1	10
	Adult	10,740*	324	7	0·1–0·05	10
Female	Adult	9,560	492	5		

* Number at adult in male greater than at newborn. P = < 0·001, with 19 degrees of freedom.

from six weeks to adult. However, the fibre number increased by the significant figure of about 45 % from newborn to adult. The number of fibres counted in the adult female lateral pterygoid muscle was slightly smaller than in the male but the difference in the total between the two was not significant.

Histology

There is still a lack of unanimity in the use of terms for the hierarchy of cells in myogenesis, and the question is discussed by Fischman (1972). In this paper the terms are generally used in the sense in which they were previously employed by Rayne & Crawford (1971). It is convenient to consider the histology of the medial pterygoid muscle first of all and then to mention any respects in which the lateral pterygoid differs from it. The diameters of the muscle fibres at different ages were compared, but no attempt was made to measure them accurately because the effect of histological processing was not sufficiently assessed for this purpose.

The appearance of the medial pterygoid muscle of the newborn rat varied somewhat from animal to animal. In transverse section some muscles consisted mainly of fibres whose myofibrils were peripheral (Fig. 1), surrounding centrally placed, relatively large and palely staining nuclei with sparse heterochromatin. These were

myotubes, and some of them should probably be regarded as late ones, as the length of fibre which intervened between consecutive nuclei did not contain the central cylinder of fibril-free cytoplasm which is characteristic of earlier myotubes. In other newborn rats the muscles were slightly more mature in that fibres with peripherally placed nuclei predominated. In either case there were also, quite commonly, fibres containing very few fibrils, perhaps only two or three; these were myoblasts or possibly very early myotubes (Fig. 2). Such cells seemed to occur most frequently at the periphery of the muscle or at intramuscular septa.

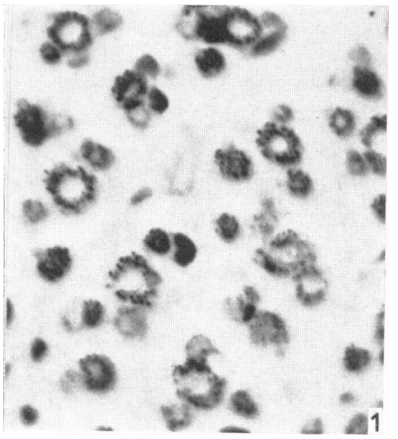
Similar features could be discerned in longitudinal sections, where in both the medial and lateral pterygoid of the newborn there were also, sometimes, lying alongside myotubes, strands of cytoplasm which did not seem to be very extended, and contained few if any myofibrils (Fig. 3). As these were generally multinucleate they would be classed as early myotubes by Holtzer (1970), whereas Boyd (1960) would have called them myoblasts. It was sometimes difficult to distinguish such structures from myofibril-free strands of sarcoplasm within myotubes. There were some cells with relatively few fibrils, which were none the less concentrated centrally, while the nuclei were peripheral: they were like embryonic myotubes with the positions of fibrils and nuclei reversed.

In view of the likely contribution of satellite cells to fibre formation the appearance of the nuclei may be significant. Most of those in the centre of myoblasts or myotubes were quite large and palely staining without much visible chromatin. When fibrils were concentrated centrally, nuclei like this were peripheral. There were also, associated with the muscle cells, smaller, darkly staining nuclei which appeared to belong to a different category from the larger ones; there were relatively few intermediate forms (Fig. 4). These smaller nuclei usually lay at the surface of the myoblasts or myotubes (Fig. 5). It was often difficult to decide whether they were within or on the outer surface of the sarcolemma. Some at least appeared to be in the latter situation, and presumably belonged to satellite cells, but only electron microscope observations could confirm this and determine whether all did so.

Sometimes at this early stage very small fibres with few myofibrils were contiguous to larger ones and appeared in transverse histological sections as though they were incompletely separated from each other by sarcolemma (Fig. 6). This was interpreted by earlier workers such as Felix (1889) as new small fibres splitting longitudinally from larger ones. This interpretation has been supported by some recent observers including Carr (1931), Lobyntsev (1960) and Hall-Craggs (1970).

The lateral pterygoid muscle of the newborn rat appeared slightly more mature than the medial (Fig. 7). Thus in an animal where the medial pterygoid consists mainly of myotubes with central nuclei, the majority of fibres of the lateral pterygoid would have peripherally situated nuclei. The fibres of the lateral pterygoid also appeared to contain rather more myofibrils at this stage. In other respects, however, the two muscles did not differ qualitatively and the lateral had similar early muscle cells to the medial (Fig. 8).

During the next few days many of those nuclei which were centrally placed in the fibre moved to the periphery without, however, leaving a central zone of cytoplasm free of myofibrils. In the medial pterygoid muscles of some two day old animals, fibres with centrally placed nuclei and fibres with peripheral nuclei seemed to occur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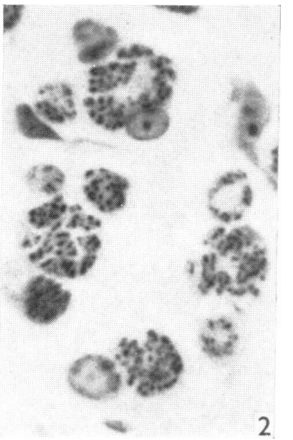
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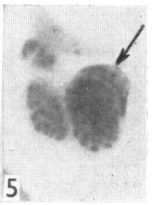
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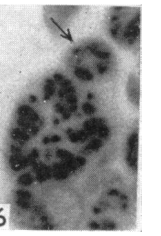
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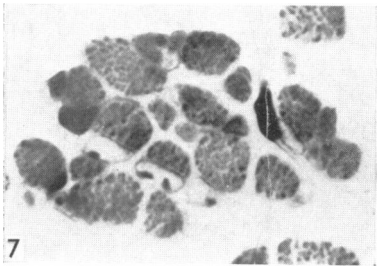
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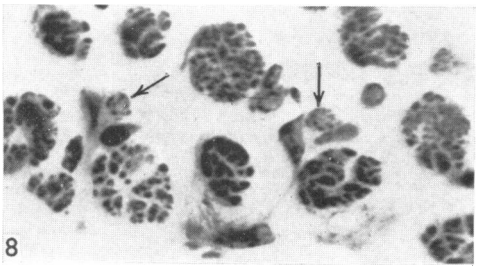
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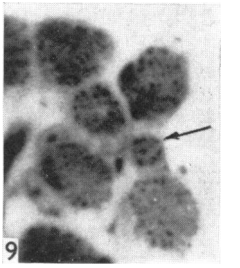
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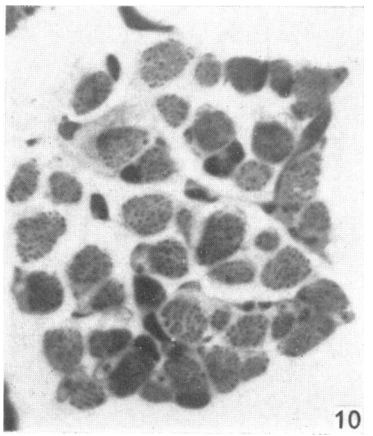
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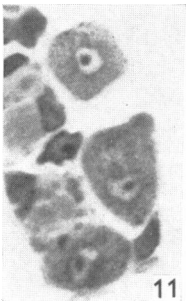
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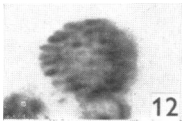
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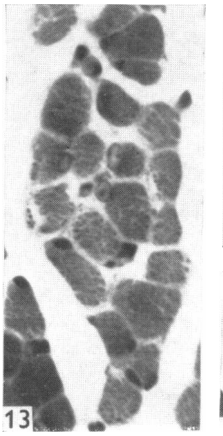
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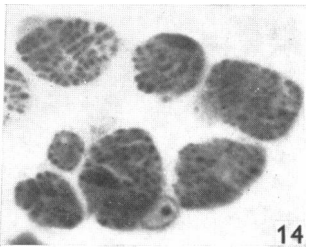
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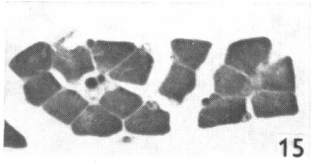
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with equal frequency. The presence of small immature muscle cells with few myofibrils indicated that new fibres were being formed during the first week after birth.

By the end of the first week, when counts showed that the period of rapid increase in fibre numbers was coming to an end, the nuclei of most of the fibres were peripheral. The fibres in general did not seem to have grown much in width and there was a fair proportion of small fibres (Fig. 9). However, there were generally more myofibrils in each fibre and they were in consequence more closely packed (Fig. 10). This gave the muscle a more mature appearance. Relatively few fibres retained centrally placed nuclei, but some were found in both the medial and lateral pterygoids (Fig. 11) and there were also occasional muscle cells which were much less well developed and contained few myofibrils. Such immature fibres could occur anywhere in the muscle, but they were commoner near the epimysium or next to the septa, where they tended to be grouped together. This does not necessarily indicate that new fibres were being formed, because fibres which were ending in a septum might look immature in transverse section because of the accumulations of centrally placed nuclei at the growing ends of the fibre.

At this stage the fibres of the lateral pterygoid (Fig. 13) were still ahead of the

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Fig. 1. Transverse section of medial pterygoid muscle of newborn rat showing typical group of myotubes of varying size. × 730

Fig. 2. Transverse section of medial pterygoid muscle of one day old rat showing group of muscle fibres of varying size and myofibrillar content. × 1260.

Fig. 3. Longitudinal section of lateral pterygoid muscle of newborn rat with a multinucleate myofibril-free strand of sarcoplasm alongside a striated muscle fibre. × 690.

Fig. 4. Longitudinal section of lateral pterygoid muscle fibre of newborn rat with two palely staining nuclei and two smaller darkly staining nuclei at the fibre's surface. × 1000.

Fig. 5. Transverse section of medial pterygoid muscle fibre of four day old rat with a nucleus (arrow), presumably that of a satellite cell, at its surface. × 1600.

Fig. 6. Transverse section of medial pterygoid muscle of one day old rat with a small fibre (arrow) which appears as though it might be splitting longitudinally from a larger contiguous one. × 1600.

Fig. 7. Transverse section of lateral pterygoid muscle of newborn rat showing typical group of muscle fibres of varying size. × 1060.

Fig. 8. Transverse section of lateral pterygoid muscle of newborn rat showing two small fibres (arrows) containing sparse myofibrils. × 1240.

Fig. 9. Transverse section of group of fibres of varying size, including one (arrow) which contains few myofibrils, from medial pterygoid muscle of seven day old rat. × 1570.

Fig. 10. Transverse section of typical group of fibres from medial pterygoid muscle of seven day old rat. × 860.

Fig. 11. Transverse section of muscle fibres with centrally placed nuclei from lateral pterygoid muscle of seven day old rat. × 1210.

Fig. 12. Obliquely transverse section of myotube of medial pterygoid muscle of fourteen day old rat. × 1480.

Fig. 13. Transverse section of typical group of fibres from lateral pterygoid muscle of seven day old rat. × 610.

Fig. 14. Transverse section of group of fibres of varying size including one small one from medial pterygoid muscle of fourteen day old rat. × 1180.

Fig. 15. Transverse section of typical group of fibres from medial pterygoid muscle of twenty-nine day old rat. × 380.

medial in their development, as evinced by their somewhat greater girth and greater number of myofibrils.

The developments which occurred in the muscle at the end of the first week were accentuated by the end of the second. The increase in the number of fibrils without corresponding increase in fibre diameter gave the fibres a still more compact appearance in transverse sections. Fibres with centrally placed nuclei did occur (Fig. 12) but they seemed to be almost entirely at the septa and adjoining part of the epimysium. At this stage there persisted a fair range of fibre diameters, some fibres being still quite thin (Fig. 14). Moreover, the fibres of the lateral pterygoid were generally somewhat larger than those of the medial and contained more myofibrils.

The predominant trend in the development of the muscles from two weeks onwards was simple enlargement of the fibres. By three weeks the fibre diameter may have doubled. The myofibrils were closely packed and almost all had peripheral nuclei. Only rarely were there fibres with central nuclei, and even these usually had myofibrils as closely packed as the others. Less mature fibres with fewer fibrils did occur here and there, but there was no evidence in support of the formation of entirely new fibres at this stage.

By the end of the first month after birth the fibres were much more uniform in diameter than they were earlier. There were few fibres with central nuclei, even at the epimysium and septa, and hardly any which showed gross evidence of immaturity. The general appearance of the muscle was now similar to that in the adult (Fig. 15).

DISCUSSION

The number of fibres in the medial pterygoid muscle of the male rat doubles during the first six weeks after birth; that of the lateral pterygoid increases by nearly half. Morpurgo (1898) and Stingl (1972) found increases, albeit smaller ones, in M. radialis and spinotrapezius of the rat; however, Enesco & Puddy (1964) found no such increase in various muscles of this animal's fore- and hindlimbs. The results of the latter authors might perhaps be criticized for failure to take into account the architecture of the muscles. However, it is of course possible that the different muscles may differ in their mode of growth, perhaps related to functional requirements just after birth. The demands on the pterygoid muscles, for instance, may well be relatively small during the suckling period. In this respect the quokka (Bridge & Allbrook, 1970) is instructive. Its forelimb is much more developed than its hindlimb at birth, so that it may climb into the pouch, and the fibre numbers of a forelimb muscle increase relatively less after birth than do those of a hindlimb muscle. The most thorough investigation failing to show an increase in the number of fibres after birth is that of Rowe & Goldspink (1969) who studied various muscles of the mouse.

It ought not to be surprising that the fibre number of some muscles of certain animals increases during growth, whereas that of others does not, because the degree of maturity at birth varies considerably from species to species. The increase in fibres found in the present investigation cannot be discounted on the grounds that immature fibres were omitted because in fact *all* fibres were counted. The significant drop in the fibre numbers of the medial pterygoid between six weeks and the adult

stage was unexpected and is difficult to explain: the sarcolysis which Glücksman (1951) described as occurring at an earlier stage in the development of various vertebrates was not noticed in this investigation.

The immature histological appearance of the pterygoid muscles of the neonate rat, especially the medial pterygoids, was compatible with the new formation of fibres indicated by the numerical counts. The cessation of fibre formation is probably gradual, starting with the disappearance of the earliest cells in the hierarchy, so that a high proportion of myotubes at birth should be associated with a small proportion of more primitive cells. Such primitive cells are in fact present in the form of multinucleate elongated myoblasts containing few if any myofibrils (early myotubes in the terminology of Holtzer, 1970). The longitudinal strands without myofibrils arise from the fusion of mononucleate myoblasts. At this early stage some of the spindle-shaped cells between the fibres may very well be pre-myoblasts. Thus immediately after birth it is likely that all stages of myogenesis are present: this was also the conclusion of Chiakulas & Pauly (1965) and Kelly & Zacks (1969).

As growth proceeds the counts indicated a decrease in new fibre formation and this was reflected in a diminution in the number of the earlier cell types. By seven days after birth early myoblasts seemed rare. However, relatively early forms of muscle fibre with few fibrils and myotubes were more common, and this, together with the considerable range of fibre diameters, was suggestive of new fibre formation. At fourteen days the absence of the earlier cell types, and the more homogeneous population of fibres, concurred with the decrease in fibre formation indicated by the counts. Chiakulas & Pauly (1965) similarly found myoblasts in various muscles of the rat during the first three weeks after birth, but not subsequently.

However, at later stages and even in the adult, new fibre formation remains a possibility, and not only by cells derived from damaged muscle fibres. Thus Shafiq (1970) and Holtzer (1970) consider that satellite cells may give rise to muscle fibres during regeneration. Ishikawa (1970) suggests that satellite cells may form myotubes during normal muscle development in addition to contributing to the latter by fusing with existing muscle fibres as described by Shafiq *et al.* (1968), Venables & Lorenz (1970) and Allbrook, Han & Helmuth (1971). The smaller nuclei with marked chromatin seen at the surface of the muscle fibres of both newborn and older rats have the appearance of satellite cell nuclei (Venables & Lorenz, 1970; Allbrook *et al.* 1971; Ontell, 1974). Such cells may contribute to the strands of cytoplasm with few myofibrils which occur in the neonate.

SUMMARY

The total numbers of fibres in transverse histological sections of the pterygoid muscles of Lister rats of various ages were counted on enlarged photomicrographic prints. The number in the medial pterygoid of the male doubled between birth and six weeks. This was followed by a decrease of rather more than 10 % in the numbers between six weeks and the adult stage in both males and females. The number of fibres in the lateral pterygoid of the male increased by about 45 % between birth and the adult stage. There were about 15 % fewer fibres in the medial pterygoid of the adult female than in the male; no such sex difference occurred in the lateral pterygoid.

Early precursors of muscle fibres were seen in histological sections of these muscles in the newborn, confirming new fibre formation after birth. Such precursors gradually disappeared, starting with the most primitive, so that by the age of four weeks the muscles had a mature appearance.

The authors are greatly indebted to Mr D. Coldham for his technical assistance.

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