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A comparison of the structural features of muscle fibres from a fast- and a slow-twitch muscle of the pelvic limb of the cat

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INTRODUCTION

The mammalian motor unit consists of a large motor nerve cell and the muscle fibres innervated by its axon. In a number of mammals it is possible to distinguish between anatomical muscles which contain a predominance of fast-twitch motor units (fast-twitch muscles) and those in which motor units with a slow speed of contraction predominate (slow-twitch muscles).

These differences in the speed of contractile response become apparent during early postnatal development and growth, and are maintained in the adult animal. In the species most studied (rat, cat) the factors responsible for these differences may be modified even in the adult animal, as cross-innervation of these muscle types has shown (Buller, Eccles & Eccles, 1960*a*, *b*; Buller & Lewis, 1965; Close, 1965*b*, 1969; Buller, 1970).

In attempting to determine the exact nature of the factors responsible, it is necessary to make comparisons, whether anatomical, biochemical or physiological, not only between fast- and slow-twitch muscles, but also between the units of contractile force within each muscle, that is, the sarcomeres. Following the example of Close (1964, 1965*a*, *b*, 1967, 1969), in relating contraction speeds of whole (rat) muscles to the sarcomere level, we have studied a typical fast- and a slow-twitch muscle in the pelvic limb of the cat. The medial head of the deep digital flexor was used as an example of a fast-twitch muscle. This muscle has been termed 'flexor hallucis longus' or 'FHL' by previous workers (Buller, Eccles & Eccles, 1960*a*, *b*). We suggest that this nomenclature should be reserved for the larger lateral head of the deep digital flexor. The correct anatomical name of the medial head of the deep digital flexor is 'flexor digitorum longus' (FDL) (*Nomina anatomica Veterinaria*, 1968) and the nomenclature is retained in this paper. The soleus was used as an example of a slow-twitch skeletal muscle.

Muscle fibres were dissected from whole muscles which had been fixed at optimal length for an isometric twitch. The number of sarcomeres per fibre was counted, and the length of each fibre compared with the length of the whole muscle.

METHOD

Setting-up the muscles: fixation and maceration

Adult cats, weighing 2–3 kg, were anaesthetized with Nembutal (pentobarbitone sodium) and their pelvic limbs dissected so as to expose the soleus and FDL muscles. A hook was tied to the tendon of insertion of each muscle (within 1 mm of the termination of muscle fibres). The animals were mounted in a frame, the hind limbs being so arranged that the soleus and FDL muscles were immersed in a paraffin pool enclosed by skin flaps. Muscles were stimulated via their (cut) motor nerves, and stretched to their optimal lengths for an isometric twitch (the length at which the twitch tension is maximal), at 36·5 to 37·5 °C, by hooking them to Statham strain gauges fixed to micrometer stages.

Having set the muscle to its optimal length for an isometric twitch, the length of each muscle, from the exposed termination of muscle fibres at its origin to the point of attachment of the hook to the tendon of insertion, was carefully measured.

The muscles were then fixed *in situ*. The deeply anaesthetized animal was killed by intravenous injection of 80 ml of 10 % neutral formol saline. Neutral formol saline solution of the same concentration was also substituted for the paraffin in the pools enclosed by skin flaps; the muscles were kept attached to the strain gauges, in the intact animal, for at least 12 hours. The tibia and fibula with the attached muscles were then removed from the animal and tied to wooden splints; the muscles were maintained at their previously measured optimal lengths by means of cotton connecting the hooks to the splints. No adjustment of whole muscle length was necessary, or could be made, as they were already stiff. They were then immersed in 10 % neutral formol saline for another 36–42 hours. The hooks were removed, and the muscles, together with the tibia and fibula, were retied to the wooden splints before maceration in 25 % (v/v) nitric acid at room temperature for 4–5 days (to soften connective tissue). The muscles, still tied to wooden splints, were stored in 50 % glycerol solution, awaiting dissection. This method was based on that described by Close (1964).

A further measurement of whole muscle length was made within one day of immersion in 50 % glycerol. Each muscle was measured from its origin to the point where the hook had been attached. Any shrinkage of the muscle, due to fixation and maceration, was recorded.

Dissection of the muscle fibres

Each muscle was laid on a flat dish, and kept moist by the administration of drops of 50 % glycerol solution. Bundles of muscle fibres were dissected, using a pair of straight surgical needles (Superfine, No. 1, round-bodied) under a binocular dissecting microscope (Zeiss, OPMi I; magnification ×6 to ×40). Each bundle was transferred to a glass slide and covered by a few drops of the glycerol solution; further dissection of the bundle then exposed single muscle fibres. Each fibre was arranged as straight as possible on a glass slide, and covered with a glass coverslip, using 50 % glycerol solution as the mounting medium. Fibres were viewed through either of two monocular microscopes (maximum magnification × 495 or × 680 respectively without oil immersion). Each fibre was accepted for measurement and counting only if both origin and insertion ends were clear and complete with some remaining con-

nective tissue, and the sarcomeres were distinct. Sarcomeres were viewed (and later, counted) using phase-contrast, or an ordinary microscope with the condenser iris shut down. No two muscle fibres from within the same bundle were accepted for measurement and counting. The classification of each muscle into a number of regions, each represented by a number of muscle fibres, will be described when considering some structural features of the muscles (see Results).

Measurements of length and sarcomere counts

The length of each fibre was measured using eyepiece graticule cross-lines and microscope micrometer stages (under magnifications of 110 or 170). A map of the course of the fibre on the glass slide was constructed upon millimetre graph paper, and the number of sarcomeres in each fibre was counted. Each sarcomere (the most distinct region being the A-band) was recorded on a mechanical hand-held counter as its image passed beneath a vertical line marked in an eyepiece graticule. During the counts, the maximum magnifications of $\times 495$ or $\times 680$ were used.

On several occasions we measured and counted the same muscle fibre as a check. Measurements of fibre length did not differ; differences in values of the total number of sarcomeres were usually of the order of 5 % and never exceeded 7 %. Such orders of difference were seen whichever of the two microscopes was used.

Preliminary experiments were identical in maceration, dissection, measuring and counting techniques. They differed in that, subsequent to setting the muscle to its optimum length for an isometric twitch and measuring its length, the animal was killed by an overdose of Nembutal and the tibia and fibula, with the attached muscles, were removed immediately. Each muscle was set to its previously measured optimal length by cotton connecting the hook to the splints; this was followed by immersion in 10 % neutral formol saline for at least 48 hours. The procedure was unsatisfactory as a means of ensuring each muscle was set and fixed at its optimal length. Some of the data obtained are relevant to this paper, and will be included, since they contribute to certain of the present findings.

RESULTS

Some anatomical and structural features of the muscles

Both muscles arise from the caudal surface of the proximal extremities of the tibia and fibula; they are flattened on what we shall consider to be their cranial and caudal surfaces (Fig. 1).

Soleus

The muscle originates via connective tissue fibres from the lateral surface of the head of the fibula, and by tendinous fibres from the proximal two-fifths of the caudal border of the fibula. Insertion is via a short tendon which joins the fused tendons of the two heads of gastrocnemius, forming a common tendon, attached to the calcaneus, which causes plantar flexion of the foot. The soleus (in 2–3 kg cats) is on average 75 mm in length, compared to the 60 mm of FDL.

The structure of the soleus muscle in the cat has been described most recently by Rack & Westbury (1969). As the cranial surface of the muscle is affixed to the caudal

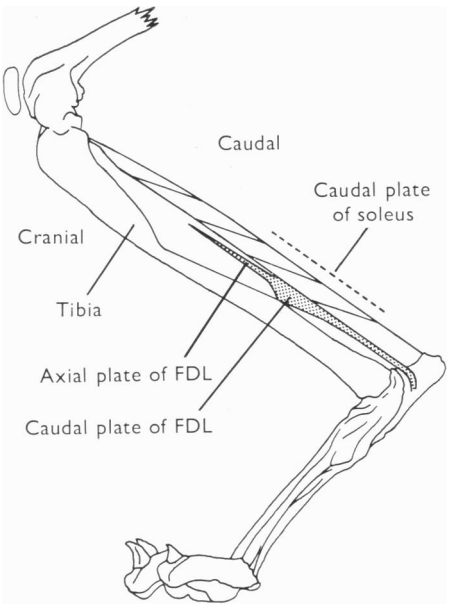

Fig. 1

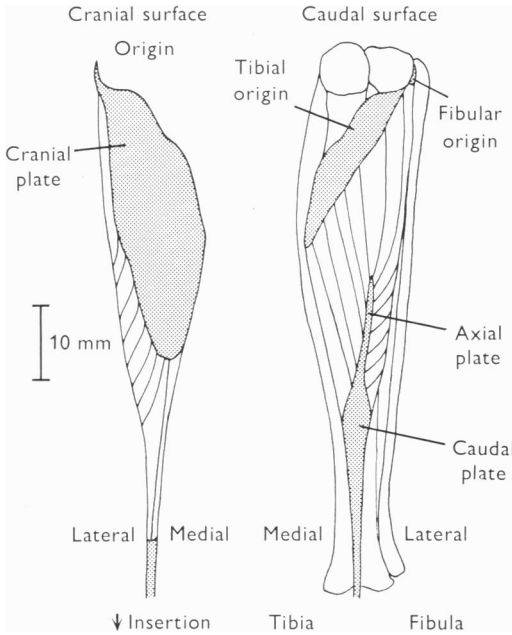

Fig. 2

Fig. 1. Diagrammatic representation of the right pelvic limb of the cat, viewed from its medial aspect. Note the caudal surface of the FDL muscle is medial.

Fig. 2. Diagrammatic representation of the gross structure of FDL muscle; lines indicate the orientation of muscle fibres.

surface of the fibula, the aponeurosis of origin may be termed the *cranial* plate of the muscle. Parallel bundles of muscle fibres pass downwards and backwards to a plate of tendinous connective tissue which covers the caudal surface of the lower half (or more) of the muscle, and may be termed the *caudal* plate. Bundles of fibres extend over the whole distance between the tendon plates and each of the plates extends over at least half the length of the muscle.

Nine fibres were dissected from each soleus muscle; the muscle was considered to consist of three parts, along its length. Three muscle fibres were taken from the proximal part; three from the region of the insertion, and three from the 'middle third' of each muscle. At each 'third', one fibre was taken from the cranial surface, one from the caudal surface, and the third from deep within the mass of muscle fibres.

Flexor digitorum longus (*Medial head of deep digital flexor*)

The muscle takes origin from the proximal extremities of the tibia and fibula (Fig. 2). The more medial aspects of the muscle originate from connective tissue attached to the caudal surface of the proximal end of the tibia (i.e. a *cranial* plate of connective tissue on FDL) and from an aponeurosis between the tibia and tibialis caudalis. The tibial origin of the muscle is covered by the popliteus muscle (not shown in Fig. 2). Laterally, the muscle takes origin from connective tissue between the medial

surface of the head of the fibula, and the lateral condyle of the proximal end of the tibia. The muscle overlies the tibialis caudalis and the origin of the true flexor hallucis longus, which forms the larger part of the deep digital flexor muscle. It is important to note that the FDL muscle is inclined on the tibia, so that its caudal surface is actually the medial surface. The same convention as for the soleus muscles (cranial and caudal surfaces) will be used, in order to ease comparison of the structure of the two muscle types.

The muscle has a long tendon of insertion, which passes downwards to join with the tendon of the flexor hallucis longus at the level of the metatarsals, where the common tendon of the deep digital flexor is formed.

FDL has a more complex arrangement of muscle fibres than that seen in soleus. Fibres originate from the medial (tibial) origin, and the lateral (fibular) origin of the muscle as described above, and pass downwards and backwards to the distal end of the muscle, which consists most noticeably of a *caudal* plate of longitudinally arranged connective tissue fibres (as in soleus). Proximal to this caudal plate, there is a longitudinal 'band' of connective tissue fibres, visible at the caudal surface of the muscle, but also present deep within the mass of the muscle. This '*axial* plate' of connective tissue appears to delimit muscle fibres of fibular from those of tibial origin, although the delimitation is by no means exact (Fig. 2). Muscle fibres near the longitudinal axis of the muscle, whether deep or superficial, pass either to the medial or to the lateral side of the 'axial plate', to insert. (It is important to note that the 'axial plate' is not so distinct as either the cranial or caudal plate; it lacks connective tissue interconnections between the longitudinal tendinous strands, so characteristic of the plates at the origin or insertion of the muscle.)

Therefore, at the distal end of the muscle there are

(i) muscle fibres of more medial origin, passing to the caudal plate;

(ii) muscle fibres near the longitudinal axis of the muscle, passing to the 'axial plate';

(iii) muscle fibres of more lateral origin, passing to the more lateral aspects of the caudal plate.

In the lateral aspects of FDL superficial fibres connecting with the more lateral part of the caudal plate take origin on the cranial surface of the muscle.

Due to the complexity of the structure of FDL care was necessary to ensure that fibres were dissected from all parts of the muscle. At most, eight fibres were dissected from each muscle, one from each of the deep and superficial layers of the cranial, caudal, medial and lateral aspects of each muscle.

Length of muscle fibres

Muscle fibres dissected from soleus muscles set at their optimal lengths for an isometric twitch were up to twice the length of FDL fibres, set up under the same conditions (Fig. 3). Not only were the fibre lengths in soleus muscles longer, but the slow-twitch muscles had a wider distribution of fibre lengths about the overall mean value (Table 1). The percentage variability in fibre lengths about the overall mean (Fig. 3) and the coefficient of variation of fibre length (Table 1) are greater in the slow-twitch muscles. The range of values of mean muscle fibre length per whole muscle is larger in the soleus than FDL (Table 2).

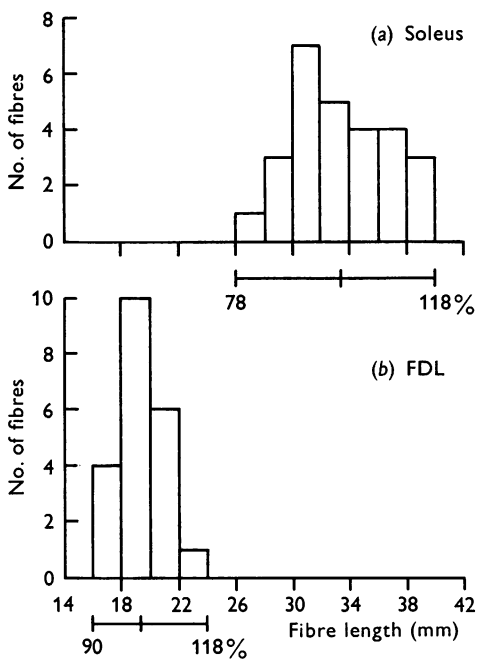

Fig. 3

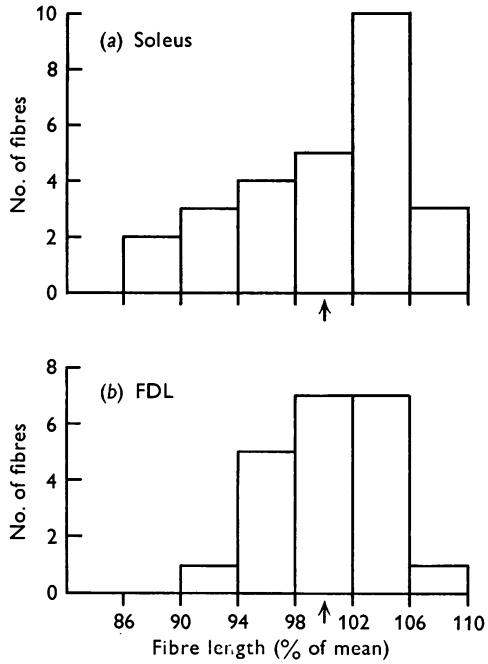

Fig. 4

Fig. 3. Histograms of the lengths (in mm) of muscle fibres dissected from whole muscles. (*a*) soleus muscles. (*b*) FDL muscles. Percentage distributions about the overall fibre mean length are given beneath each histogram. Note that in these, and all subsequent histograms, results are from 27 soleus and 21 FDL muscle fibres (Table 1).

Fig. 4. Histograms of the lengths of muscle fibres within each muscle expressed as a percentage of the mean fibre length for the muscle. Each histogram is compounded from the results of several muscles. (*a*) Soleus muscles. (*b*) FDL muscles.

Variability of lengths of muscle fibres within each muscle

In both soleus and FDL no particular region of any individual muscle was found to contain muscle fibres of lengths consistently different from those in any other region. Fig. 4*a* and 4*b* compare the range of lengths of muscle fibres within the slow- and fast-twitch muscles. Each muscle was represented by a number of fibres, the lengths of which are expressed as a percentage of the mean fibre length for the muscle; each histogram is compounded from the results of several muscles. The FDL muscles had fibre lengths which lay between 90 and 110 % of the mean values; soleus muscle fibres showed slightly greater variability, fibre lengths being between 86 and 110 % of the means. The overall mean fibre length of soleus muscles was about 1½ times that for FDL muscles (Table 1), and thus soleus fibre lengths are distributed about larger mean values (100 % in Fig. 4*a*), and the absolute variability of fibre lengths within a soleus muscle appears to be the greater (Table 2).

Number of sarcomeres in series within muscle fibres

Soleus muscle fibres contained, on an average, almost twice as many sarcomeres in series as did the FDL fibres (Table 1). The variability in the number of sarcomeres

Table 1. *Muscle fibre lengths, sarcomere lengths and whole muscle lengths in soleus and flexor digitorum longus muscles (after fixation and maceration) at optimal length for an isometric twitch*

	Soleus			Flexor digitorum longus		
Number of muscles dissected	3			4		
Number of fibres dissected	27			21		
	Mean	S.D.	Coefficient of variation (%)*	Mean	S.D.	Coefficient of variation (%)
Muscle fibre length (mm)	33·52	3·34	9·96	19·44	1·35	6·94
Number of sarcomeres per muscle fibre ($\times 10^3$)	12·91	2·38	18·43	7·099	0·46	6·48
(Mean) sarcomere length per muscle fibre (μm)	2·63	0·23	8·75	2·74	0·12	4·38
Muscle length (mm) after fixation and maceration	75·50	7·47	9·89	62·75	8·85	14·10
Shrinkage (mm) due to fixation and maceration	0·83	0·76	91·57	0·75	0·96	128·0
Fibre length as a fraction of (shrunk) muscle length	0·444	0·024	5·41	0·321	0·032	9·97

Table 2. *Variability in the number of sarcomeres per muscle fibre, and in muscle fibre lengths, within a given soleus or flexor digitorum longus muscle*

Number of fibres representing a muscle	Number of sarcomeres per fibre ($\times 10^3$)			Muscle fibre lengths per whole muscle (mm)		
	Mean	S.D.	Coefficient of variation	Mean	S.D.	Coefficient of variation
			Soleus muscles			
9	10·414	0·407	3·91			
9	9·702	0·860	8·86	Preliminary experiments		
9	14·330	0·783	5·46			
9	15·476	1·973	12·75	37·07	1·67	4·51
9	10·772* L	0·671	6·23	30·52	1·87	6·13
9	12·483* R	1·106	8·86	32·97	2·34	7·10
			FDL muscles			
8	6·660	0·512	7·69			
8	6·919	0·266	3·84	Preliminary experiments		
8	7·069	0·351	4·97			
8	7·346	0·381	5·19	20·63	1·15	5·57
5	6·721* L	0·256	3·81	18·61	0·87	4·68
5	6·881* R	0·476	6·92	18·18	0·50	2·75
3	7·435	0·374	5·03	19·73	0·49	2·48

* From the same animal. L or R = left or right.

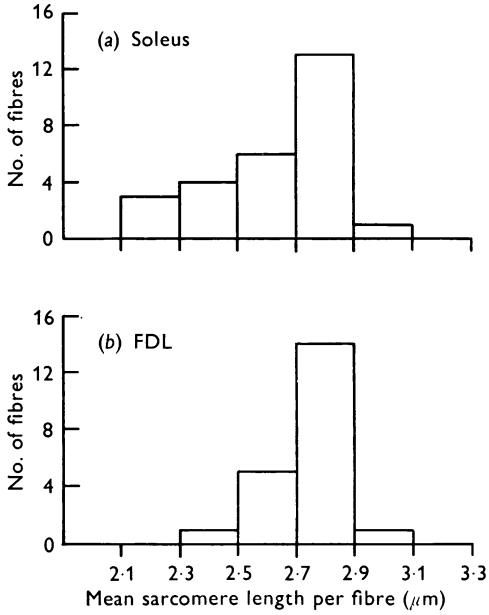

Fig. 5

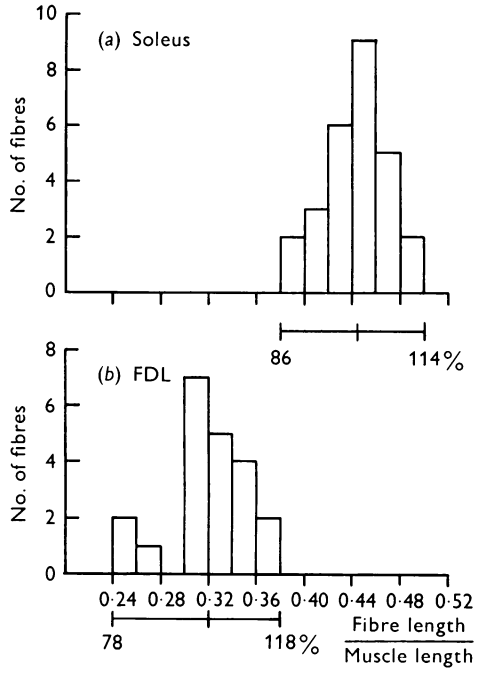

Fig. 6

Fig. 5. Histograms of the values of mean sarcomere length per muscle fibre in whole muscles. (*a*) Soleus muscles. (*b*) FDL muscles.

Fig. 6. Histograms of muscle fibre lengths expressed as fractions of (post-fixation and post-maceration) muscle lengths in whole muscles. (*a*) Soleus muscles, (*b*) FDL muscles. Percentage distributions about the overall mean fraction for each muscle type are given beneath each histogram (see table 1).

comprising a soleus muscle fibre was approximately three times the variability within FDL muscles (Table 1). Such differences between the two muscle types were confirmed on examining the mean number of sarcomeres in series for each whole muscle dissected (Table 2). FDL muscles showed remarkably little variability from muscle to muscle; values of the number of sarcomeres per muscle fibre within muscles did not differ significantly ($P > 0{\cdot}1$) from muscle to muscle. Soleus muscles had significantly different values of number of sarcomeres in series ($P < 0{\cdot}001$).

Sarcomere counts on two muscles from the same animal were carried out for both muscle types (Table 2). The numbers of sarcomeres comprising muscle fibres were significantly different in the pair of soleus muscles ($P < 0{\cdot}01$), whereas the results of counts on the pair of FDL muscles were extremely similar ($P > 0{\cdot}1$).

The results of some preliminary experiments have been included in Table 2, as the inadequacy of the earlier experimental method of maintaining the muscle fibres at their optimal lengths does not invalidate the counts of number of sarcomeres within each fibre.

Mean sarcomere length per muscle fibre

For each muscle fibre dissected, measured and counted, a value of mean sarcomere length was calculated by dividing the length of the fibre by the number of sarcomeres in series. The average values of mean sarcomere length per fibre were similar in the two muscle types (Fig. 5; Table 1). Soleus muscles exhibited greater variability in mean sarcomere length per fibre (Table 1).

Fibre length as a fraction of whole muscle length

Fibre lengths were expressed as fractions of the lengths of the anatomical muscles from which they were dissected (Fig. 6). Muscle length was taken to be the length measured after fixation and maceration (Table 1); shrinkage due to these processes was approximately 2·5 % of the initial length of both muscle types; no determination was made of the amount of differential shrinkage between muscle fibres and connective tissue.

Soleus muscle fibres were found to comprise approximately 0·4 of the length of the whole muscle (Table 1), so confirming the observation of Close (1965*a*), and muscle fibres within FDL were found to be approximately 0·3 of whole muscle length. FDL muscle fibres exhibited greater variation about this mean value (Table 1; Fig. 6). As FDL muscle fibres vary less in length than soleus muscle fibres (Figs. 3, 4), this greater variation in fibre length as a fraction of whole muscle length reflects a greater variation in whole muscle length for all FDL muscles dissected (Table 1).

DISCUSSION

Comparison of the mean values of sarcomere length per fibre for soleus and FDL muscles shows (Table 1) that the muscle types were extremely similar; this is the same conclusion as reached by Close (1964) in comparing mean sarcomere lengths per fibre in rat extensor digitorum longus and soleus muscles (fast- and slow-twitch muscles, respectively). A knowledge of the distribution of sarcomere lengths along such muscle fibres would lead to a knowledge of the contribution each sarcomere makes to the tension produced by a muscle fibre, and its speed of contraction during the active state, as the tension produced by a sarcomere is dependent upon the overlap of its actin and myosin filaments (Gordon, Huxley & Julian, 1966). The mean sarcomere length per muscle fibre gives no information about the range of sarcomere lengths within one muscle fibre; we cannot, therefore, compare soleus and FDL in this respect.

The purpose of these experiments was to obtain at least some of the information necessary to enable the contraction speeds of the whole muscle to be related to the speed of contraction at each sarcomere. It is necessary to know:

(i) the number of sarcomeres in series along the muscle fibres;

(ii) the arrangement of muscle fibres relative to the longitudinal axis of the muscle, along which it contracts;

(iii) the amount, and properties of, the connective tissue in series with the muscle fibres (as well as elastic components within the muscle fibres).

Factor (i) determines the number of contractile units in series; (ii) determines how

much of the tension generated by the muscle fibres is conveyed to the tendon of insertion of the anatomical muscle. If a muscle fibre lies at an angle (α) to the longitudinal contractile axis of the muscle, the actual speed of shortening of the fibre, or the tension developed by it, is shown at the tendon of insertion as the actual speed of shortening, or tension developed, multiplied by cosine α. The angle α changes as the muscle contracts (Rack & Westbury, 1969). Factor (iii) is important in the transient contractile properties of the anatomical muscle, for example, in an isometric twitch.

FDL shows little variability as regards (i), both within a muscle and from muscle to muscle. Factors (ii) and (iii) may only be dealt with in a qualitative manner, but it has been shown that FDL has a greater complexity of arrangement of muscle fibres than does soleus. This suggests that FDL has greater variability in the angle α, from region to region within the same muscle. In an FDL undergoing contraction, the bipennate structure of the muscle is maintained by its bony attachments to tibia and fibula; hence as shortening takes place there will be an increase in α with a reduction in tension and an increase in speed of shortening as measured at the tendon. It also seems likely that FDL, as compared with soleus, contains muscle fibres which have a marked variability in the amount of connective tissue associated with each of them. Conversely, in soleus factor (ii) seems remarkably uniform within a muscle; muscle fibres appear to be arranged parallel with each other and the angle α would be expected to be more uniform than within an FDL muscle. Rack & Westbury (1969) state that the angle increases as the soleus muscle shortens, but even at the shortest lengths of the whole muscle cosine α is unlikely to be less than 0·95 (corresponding to an angle of 18°). Factor (i) varies, not greatly within one muscle but from muscle to muscle; different soleus muscles exhibit very different mean values for the numbers of sarcomeres in series (and for muscle fibre length: Table 2).

To obtain a value of speed of shortening per sarcomere in a muscle undergoing an isotonic contraction with a given load, the speed of shortening of the whole muscle may be divided by the average number of sarcomeres per muscle fibre within a muscle (Close, 1965*a*).

Such a calculation is based on several assumptions; first, that muscle fibres are of uniform length and contain a uniform number of sarcomeres in series; secondly, that the length of each sarcomere is the same; thirdly, that the muscle fibres contract along the contractile longitudinal axis of the muscle. As mentioned earlier, we can give no information about the distribution of sarcomere lengths within the muscle fibres, that is, we cannot estimate the contribution each sarcomere makes to the speed of shortening of a muscle fibre. The accuracy of the calculation for the soleus muscle is limited by the variability in the mean number of sarcomeres per muscle fibre in different muscles; for FDL accuracy is limited by the complexity of the arrangement of muscle fibres relative to the contractile longitudinal axis of each muscle.

Despite these limitations, it is hoped that the present results will enable contraction speeds of these fast- and slow-twitch muscles to be related to the level of the sarcomere, and aid comparison of these muscle types with their counterparts within other mammals.

SUMMARY

A study of some structural features of muscle fibres was made in the soleus (slow-twitch) and flexor digitorum longus (FDL, fast-twitch) muscles of the adult cat.

The FDL muscle (the medial head of the deep digital flexor) has in the past been called the 'flexor hallucis longus' or 'FHL', by some workers. In the present paper, the correct anatomical name, flexor digitorum longus, is used.

At optimal length for an isometric twitch, FDL muscle fibres were approximately 20 mm in length (2–3 kg cats); soleus muscle fibres were on average $1\frac{1}{2}$ times, but could be twice as long.

Soleus muscle fibres showed marked variation in the total number of sarcomeres in series, particularly in different muscles, whereas FDL muscle fibres contained about 7000 sarcomeres in series in all muscles studied.

At optimal length for an isometric twitch, both muscle types had mean sarcomere lengths distributed about 2·6–2·7 μm.

Soleus muscle fibres comprised about 0·4 of the whole muscle length; FDL muscle fibres were only about 0·3 of the whole muscle length.

The muscle types were compared as regards the results given above, and these results viewed in the light of factors relating the speeds of contraction of whole muscles to the speeds of contraction of single sarcomeres.

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