THE MORPHOLOGY OF INTRAFUSAL MUSCLE FIBRES
IN THE CAT

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It has long been recognized that the muscle spindle is composed of muscle fibres of large and small diameter (see e.g. Sherrington, 1894; Cuajunco, 1927, 1940), but the claim that the fibres branch in their course through the spindle has been a matter of controversy. Branching was held to occur by the majority of workers from Weismann (1861) to Denny-Brown (1928), though it is probable that many of the earlier claims were prejudiced by a belief that spindles served as centres of muscle growth. According to Sherrington (1894) and Ruffini (1898), large 'parent' fibres in the proximal pole of the spindle split longitudinally to form smaller 'daughter' fibres, which course through the equatorial region to taper off as long tendinous filaments in the distal pole. However, Batten (1897) and recently Häggqvist (1960) maintain that branching in one pole is followed by reuniting of the fibres in the other. Forster (1894) holds that the branching and reuniting of fibres occurs throughout the length of the spindle, and Cilimbaris (1910) adds that they also anastomose so as to form a syncitial network in the equatorial region reminiscent of cardiac muscle. Against this it has been urged (Baum, 1900; Cuajunco, 1927, 1940; Barker, 1948; Gray, 1957; Boyd, 1958; Cooper, 1960) that intrafusal fibres remain single, and that the tapering of short fibres alongside longer ones may have been mistaken for instances of branching. At a preliminary stage of the present study we became convinced that branching does occur, and it appeared to us that Forster's observations were correct (Barker, 1959). Further investigation, however, led us to the conclusion that branching is mainly exhibited by the small intrafusal fibres (Barker & Gidumal, 1960), and Boyd (1960), reversing his earlier opinion (1958), arrived at a similar conclusion. The present paper deals with this matter in detail.

METHODS

We have made the majority of observations on spindles from the rectus femoris muscle of the cat, but have also examined spindles from the teres minor, sternohyoid, 7th internal intercostal, tenuissimus, and vastus lateralis muscles of this animal. The bulk of the

material was embedded in paraffin, cut serially and transversely at 12 μ, and stained with haematoxylin and eosin. The muscles were fixed *in situ* in either Bouin's or Zenker's fluid, and were subsequently dissected out in either 70 % alcohol or water according to the fixative employed. Other material studied included longitudinal paraffin sections; transverse celloidin, 'Nonex', and frozen sections; teased gold-chloride preparations (Gairns's method); and macerated preparations in which either nitric acid, gastric juice, or collagenase was used in an endeavour to dissociate the intrafusal muscle fibres. In the application of these various methods observations were made on 246 spindles, of which twenty were of the tandem type, but of this total the most detailed information was obtained from the graphic reconstruction of thirty-two spindles (including three tandems) cut in serial transverse section. In the first five reconstructions, camera lucida drawings of the sections were made at magnifications of × 430 or × 600. Initially every section in a series was drawn, but this was later reduced to every fifth 12 μ section when it became evident that the complete process of fibre branching occupied a length of 60–90 μ. When branching was detected, however, every section in that part of the series was drawn. The drawings were then converted into a projection-plan of the spindle, at the same magnification, in which the intrafusal bundle is presented as if divided sagittally and the fibres in each half arranged in a horizontal plane. In reducing these projection-plans to more manageable dimensions, the length of the fibres was accurately represented but their width exaggerated. In reconstructions of twenty-seven further spindles sketches of every fifth section were substituted for camera lucida drawings, and projection-plans made with the aid of these and measurements of the lengths and diameters of the individual fibres. The diameters of fibres that were not circular in section were recorded as the average of their maximum and minimum widths. In a few selected instances where the bifurcation of a fibre could be demonstrated to the best advantage, serial photographs were taken using an oil-immersion objective.

RESULTS

The intrafusal bundle in single spindles from rectus femoris consists of a group of four to twelve muscle fibres in which those of small diameter and short length usually predominate over those which are larger and longer. Constant features of the bundle are its encapsulation, suspension in a lymphatic space, and changes in nucleation which occur in the equatorial region associated with the sensory innervation. The location of this region appears to be related to the position of the spindle in the muscle, and the polar regions on either side of it are usually of unequal length (Barker & Ip, 1961). There is no constant feature which is characteristic of one pole and not the other, but it is convenient to designate them as proximal and distal with respect to their orientation with the origin and insertion of the extrafusal muscle bundles. We regard a polar region of a muscle spindle as extending from the juxta-equatorial region to the furthest extremity of the origin or insertion of the muscle fibres composing it. However, the term 'spindle' is sometimes restricted by others to include only that part of the muscle bundle invested by the capsule, the polar extremities being regarded as coincident with the capsular extremities. Thus Häggqvist (1960) describes muscle fibres as entering or emerging from the spindle at one or other pole, and distinguishes between their extra- and intrafusal course. This can only lead

to confusion in view of the wide use of the term 'spindle' to denote the whole proprioceptor. Tandem spindles may be regarded as consisting of a number of single spindle units connected together by a few intrafusal fibres of large diameter which run a continuous course through the successive encapsulations.

The two main types of intrafusal muscle fibre present in all spindles are those which are large and long and possess the characteristic nuclear bag and myotube regions described by Barker (1948), and those which are small and short with a single central row of nuclei in the equatorial region (the nuclear-chain fibres of Boyd, 1960). Both length and diameter measurements of the fibres composing the intrafusal bundle are therefore bimodal. However, in some spindles there are fibres present whose
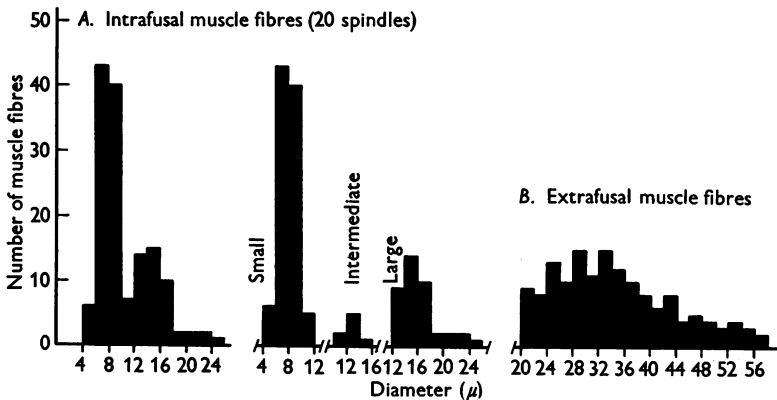
Text-fig. 1. *A*. Mid-polar diameter histograms of a sample of 142 muscle fibres belonging to 18 single and 2 tandem spindles from the rectus femoris muscle of a 2 kg cat. The histogram on the left is broken down on the right in terms of the 94 small, 8 intermediate, and 40 large fibres in the sample. *B*. Diameter histogram of a random sample of 150 extrafusal muscle fibres from the same muscle. Measurements made on Zenker-fixed transverse paraffin sections.

characteristics make it necessary to recognize a third type which we shall designate as intermediate. In a sample of eighteen single and two tandem spindles from the rectus femoris muscle of a 2 kg cat (C 50), there were ninety-four small, forty large, and eight intermediate fibres whose mid-polar diameters were 4–12μ (mean 7·5μ), 12–26μ (mean 16·9 μ), and 10–16μ (mean 12·6μ) respectively (see Text-fig. 1). The diameter range of a random sample of 150 extrafusal muscle fibres from the same muscle was 20–58μ (mean 35μ). The length of intrafusal fibres is such that the small fibres may be about half as long as the large ones. In ten single rectus femoris spindles 7·5–8·5 mm long, the length range of thirty-five small fibres was 4·0–6·1 mm, of seventeen large fibres 7·0–8·5 mm, and of five intermediate fibres 6·4–7·8 mm.

From one to three, usually two, large fibres are present in all spindles. They tend to retain the same position in the intrafusal bundle, and do not branch. Their diameter undergoes little change except at the extreme ends, where tapering occurs, and in the myotube regions, where there is typically a decrease of two or three microns. The small fibres also narrow down in the equatorial region, their diameter becoming little more than that of each vesicular nucleus in the nuclear chain. About one in five bifurcates, and the two fibres produced often reunite. If parent fibres only are counted, the number of small fibres present in a spindle is from one to eight, and is usually four or five. Their position in the intrafusal bundle undergoes frequent changes as they twist among themselves and cross over the large fibres. The intermediate type of fibre resembles the large in that it possesses nuclear-bag and myotube regions, but the bags tend to have smaller aggregations of vesicular nuclei, and the myotube regions show a more pronounced decrease in diameter. In the polar regions their variation in diameter is such that in isolated transverse sections they may easily be taken for small fibres (cf. Pl. 1, figs. 2 and 5, fibre a). They also tend to change their position in their course through the intrafusal bundle. About one out of three spindles possesses fibres of this type; usually only one is present, never more than two. They occasionally bifurcate; in one exceptional case the fibres produced were observed to reunite. While these fibres are of medium size in the intrafusal fibre diameter spectrum, a medium-sized fibre is not necessarily of the intermediate type; the equation of fibre size with fibre type in our preliminary note (Barker & Gidumal, 1960) was thus an over-simplification.

In the process of bifurcation, as seen in optimum transverse sections (see Pl. 1; Pl. 2, figs. 1–9), a small or intermediate type fibre loses its circular contour and increases in size to assume an oval shape. This becomes constricted into the form of a figure of eight before finally splitting into two. The complete process occupies a distance of 60–90μ. In the reuniting of small fibres the reverse sequence occurs. The two fibres produced by branching are usually unequal in size but their combined diameters are initially equal to that of the parent fibre. After a short distance, however, both fibres increase in diameter, the larger of the two regaining the diameter of the parent fibre. For example, a small fibre 8μ in diameter will typically branch into two fibres which initially measure 5 and 3μ in diameter, and subsequently increase to diameters of 8 and 5μ. The identity of the parent fibre thus tends to be retained after division. This is particularly marked in the case of the intermediate type fibres which branch, for when the fibres produced pass through the equatorial region the larger of the two has a nuclear bag and myotube region while

the other has a nuclear chain (see Text-fig. 2; Pl. 2, figs. 1–9). Bifurcation, with the branches running towards the equator, occurs in the proximal pole or in the proximal part of the equatorial region; in tandem spindles it occurs in the equivalent parts of the single spindle units that are linked together. When small fibres branch, the fibres produced may either continue through the intrafusal bundle and taper off, or reunite in the distal pole or distal part of the equatorial region. We have never observed a small fibre to give a distally directed branch in the distal pole, but in one instance an intermediate fibre gave rise in the distal pole to a short branch running away from the equator (see Text-fig. 4; and Pl. 1). The branching of intermediate fibres is easier to detect and to demonstrate owing to their larger size. It should be possible to obtain convincing evidence of branching from teased and dissociated material, but our attempts to do so have so far proved unsuccessful.

The process of branching or reuniting is quite distinct from the condition where one fibre tapers off alongside another (see Pl. 2, figs. 10–13). Tapering takes place over a distance of several hundred microns, the shortest length being about three times that occupied by branching or reuniting. A fibre tapers off usually over a distance of 300–500μ, but distances of up to 800μ may occur. The shortest tapering lengths tend to occur within the polar regions at the ends of the small fibres, while at the extremities of the spindle the larger fibres taper off as longer tendinous filaments. In transverse section tapering is marked by a progressive loss in diameter, and ultimately by a loss of circular contour and myofibril content. The final tendinous wisp of a small fibre usually merges with the endomysium of a larger fibre or the axial sheath, and the ends of the larger fibres merge with either tendon, aponeurosis, perimysium, or the endomysium of neighbouring extrafusal fibres.

In transverse section some of the muscle fibres composing the intrafusal bundle may exhibit Krüger's (1952) 'Fibrillenstruktur', others a 'Felderstruktur' (fibrillar and areal patterns of Gray, 1958). However, it is not possible to relate structural pattern categorically to fibre type, since the pattern does not remain the same throughout the length of each fibre. For most of their length all fibres are fibrillar, and the fibrillar pattern is evident in regions where branching or reuniting occurs. The areal pattern may occur sporadically in the polar regions, but it is characteristic of the juxta-equatorial regions. When there is a change from the fibrillar to the areal pattern it usually occurs in the majority of the fibres in the intrafusal bundle. Each fibre is usually areal for part of its length, the total distance amounting to several hundred microns, seldom more than 1 mm. In fibres of the large and intermediate types this forms only a small part of their total length so that their structural pattern is predomi-

nantly fibrillar. In small fibres the ratio of areal length to fibrillar length is higher, owing to their shorter total length, and by comparison with the large fibres they give the impression of being predominantly areal. However, the areal portions of small fibres seldom exceed 35 % of their total length, and the percentage is often considerably less. Boyd (1960) implies that large fibres are exclusively fibrillar and small fibres exclusively areal, but we have never observed this condition. It may be significant that the areal pattern appears to be most prevalent in the juxta-equatorial regions of the spindle where the motor innervation tends to be most profuse. If fibrillar and areal patterns are indicative of fast and slow

TABLE 1. Number and nature of muscle fibres belonging to eighteen spindles from cat rectus femoris

s, single fibres; bt, fibres bifurcating and tapering; br, fibres bifurcating and reuniting

| Cat	Large type s	Intermediate type			Small type			total	
		s	bt	br	s	bt	br	min.	max.
C 8	2	1	—	—	—	—	1	4	5
C 24	2	1	—	—	3	1	1	8	10
C 60	2	1	—	—	4	—	1	8	9
C 50	3	—	—	—	3	1	—	7	8
C 50	2	1	—	—	3	1	—	7	8
C 50	2	—	—	—	5	—	—	7	7
C 50	2	1	—	—	4	—	1	8	9
C 50	1	1	—	—	5	—	—	7	7
C 50	1	—	—	—	6	—	1	8	9
C 50	2	—	—	—	4	—	—	6	6
C 50	1	—	—	—	5	—	—	6	6
C 50	2	1	—	—	5	—	—	8	8
C 50	3	—	—	—	3	1	1	8	10
C 50	1	—	—	—	3	1	—	5	6
C 50	2	1	—	—	3	—	—	6	6
C 50	2	—	—	—	3	—	1	6	7
C 50	*2	1	1	—	5	3	—	12	16
C 63	1	—	1	(1)	7	—	—	9	10 (+1)
Totals	33	9	2	(1)	71	8	7	130	147 (+1)

11 (+1)   86

* Tandem spindle.

contraction, as Krüger (1952) maintains, the quickness or slowness of intrafusal muscle fibres must be a matter of degree, for in the individual fibre the two patterns are not mutually exclusive. In this connexion it may be noted that Krüger's observations on the structural pattern of extrafusal muscle fibres were made on individual transverse sections, no fibres being traced throughout their length; the same is true of Gray's (1958) study of frog muscle.

The number and nature of the muscle fibres belonging to eighteen spindles traced in transverse sections of the rectus femoris muscles of four adult cats are shown in Table 1. There are eighty-six small fibres

in the sample, of which seventy-one are single, and fifteen, or 17·4%, bifurcate. Intermediate fibres occur in ten spindles, there being a total of eleven in the sample, of which two show branching. One of these is exceptional in that the fibre branches twice, reuniting almost immediately after the first bifurcation before branching again; this sequence is shown as *br* (1) and *bt* 1 in the Table (see C63). In six spindles all the fibres are single, an intermediate fibre being present in three of them. A total of 130 single and parent fibres belong to the seventeen single spindles, an average of seven per spindle; if the fibres produced by branching are taken into account the total is 147, and the average eight. The tandem spindle in the sample is of the double kind and accounts for a maximum total of sixteen fibres, double the maximum average fibre content of a single spindle.

Many of the features of intrafusal muscle fibres so far described are illustrated in Text-fig. 2, which is a diagrammatic analysis of the intra-fusal bundle of a single rectus femoris spindle consisting of one large, one intermediate, and seven small fibres. In Text-fig. 2*A* the muscle fibres are arranged schematically side by side and enclosed within square brackets representing the equatorial encapsulation. The length of this region, in this and other figures, corresponds with the equatorial limits of the periaxial space (cf. Barker & Ip, 1961). The scale used for the width of the muscle fibres is ten times that used for length. Variation in muscle fibre diameter is shown on the basis of measurements taken at intervals of every fifth 12μ serial transverse section, and the distribution of areal, as opposed to fibrillar, pattern is indicated by shading. The small fibres remain single throughout their lengths, which range from approximately two-fifths to three-quarters the length of the large fibre. The intermediate fibre (*A*) branches twice in the proximal pole. The first bifurcation is the exceptional one already noted in Table 1, and results in two fibres of similar diameter, which rejoin after a brief course of 72μ. The second bifurcation occurs 360μ further on and is the one illustrated in Pl. 2, figs. 1–9. Of the two fibres produced, one (*a*) displays typical characteristics of an intermediate fibre in that its diameter is variable and the equatorial nucleation consists of myotube regions and a small nuclear bag, while the other (*a'*) has the characteristics of a small fibre in both diameter and equatorial nucleation (see Pl. 2, figs. 6–8). The distribution of fibrillar and areal structure in the fibres illustrates the typical prevalence of the areal pattern that occurs in the juxta-equatorial regions. In this spindle the nuclear bags and chains lie towards the distal end of the equatorial region, as is often the case. In Text-fig. 2*B* the spindle is shown in schematic projection-plan in order to illustrate the change of position of fibres in their course through the intrafusal bundle;
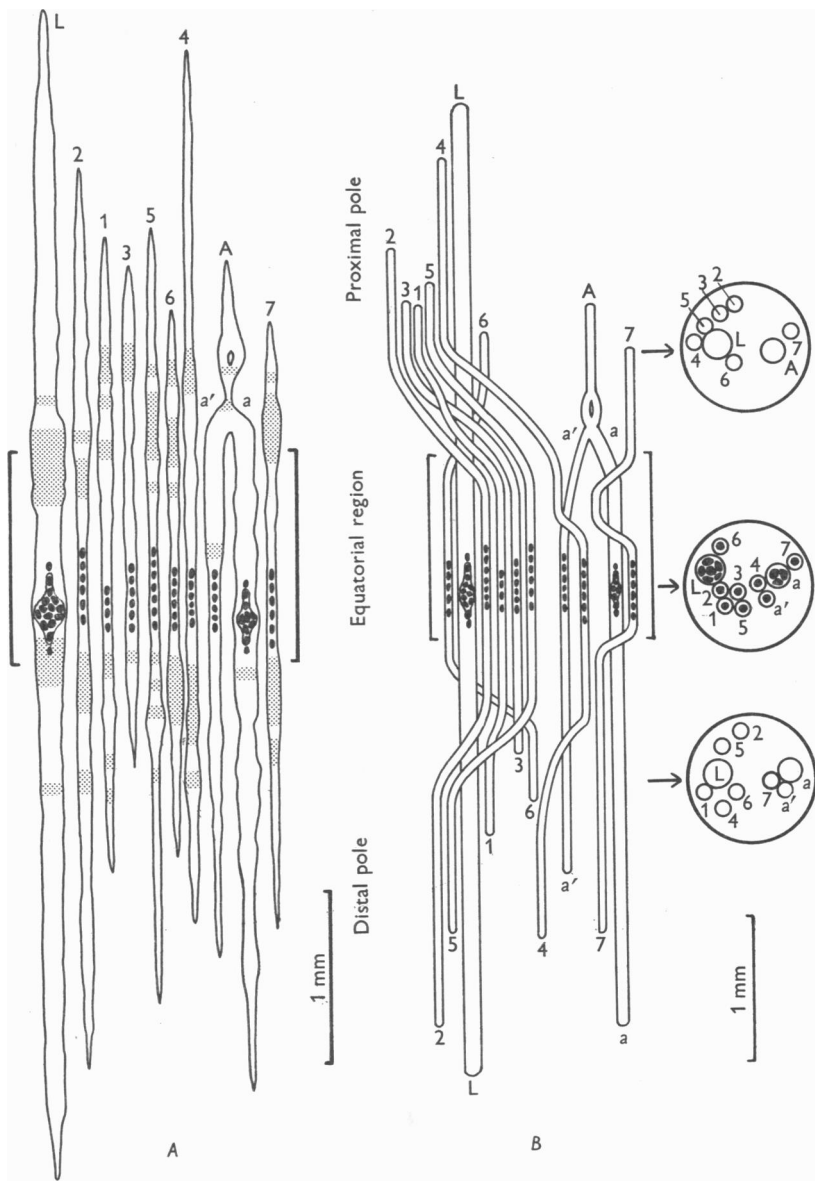
Text-fig. 2. Diagrammatic analysis of a single rectus femoris cat spindle comprising one large fibre (L), one intermediate fibre (A) bifurcating into a and a', and seven small fibres (1–7). A. Each fibre's length and level of origin and insertion is accurately shown, but scale used for width is × 10 that used for length. Diameter variation is shown on basis of $60\,\mu$ interval measurements; stippling indicates areal, as opposed to fibrillar, pattern. B. Projection-plan and three schematic transverse sections illustrating changes of fibre position; scale applies to plan only, scale for fibre width being × 8 that for length. Fibre diameters standardized as $17\,\mu$ large, $13\,\mu$ intermediate, $8\,\mu$ small. In both A and B square brackets indicate limits of equatorial encapsulation; nuclei schematic, but length of each nucleated region accurate. Compare with Pl. 2, figs. 1–9.

the appearance in transverse section is shown diagrammatically at three key levels alongside. The sinuous course of the small fibres, and the stable course of the large, are typical.
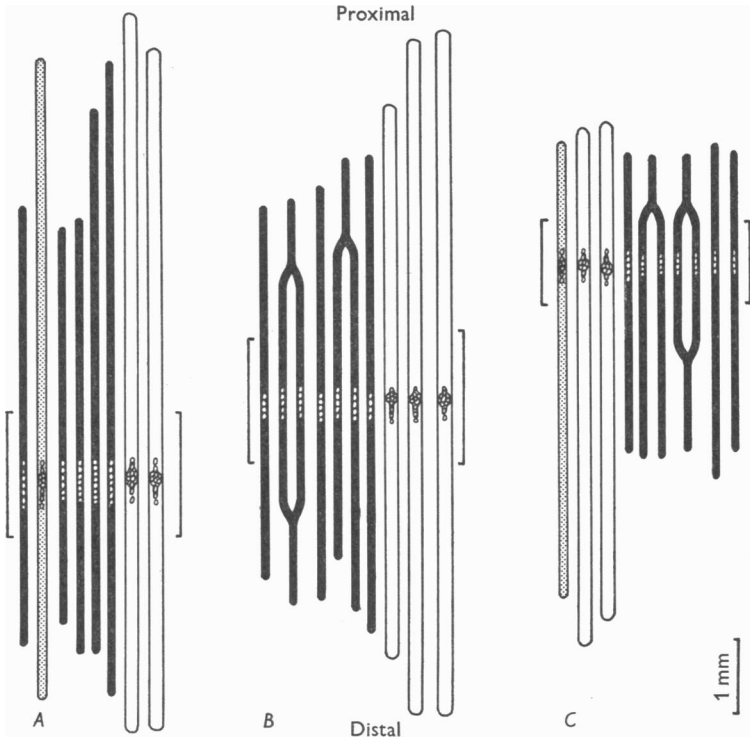
Text-fig. 3. Schematic diagrams of the fibres composing three single rectus femoris cat spindles. Large fibres white, intermediate fibres stippled, small fibres black. Fibre diameters standardized as in Text-fig. 2B, and shown on a scale × 10 that used for length. Square brackets indicate limits of equatorial encapsulation; nuclei schematic but length of each nucleated region accurate.

As a further illustration of the composition of the intrafusal bundle of single spindles, the muscle fibres of three spindles from rectus femoris are drawn in stylized form, side by side, in Text-fig. 3 *A–C*. An intermediate fibre is present in spindles *A* and *C*, but not in *B*. In *A* all the fibres are single, while in both *B* and *C* a small fibre bifurcates, and another bifurcates and reunites. Spindles *B* and *C* provide good examples of how the composition of the intrafusal bundle fluctuates at different levels owing to the different lengths of the fibres composing it and the occurrence of branching and reuniting. The maximum number of fibres is always present at mid-equatorial level.

Finally, in Text-fig. 4 a tandem spindle is illustrated in schematic projection-plan, the equatorial encapsulations being indicated as diagrammatic fusiform swellings. The tandem is of the typical double type described by Barker & Ip (1961), consisting of a small capsule enclosing
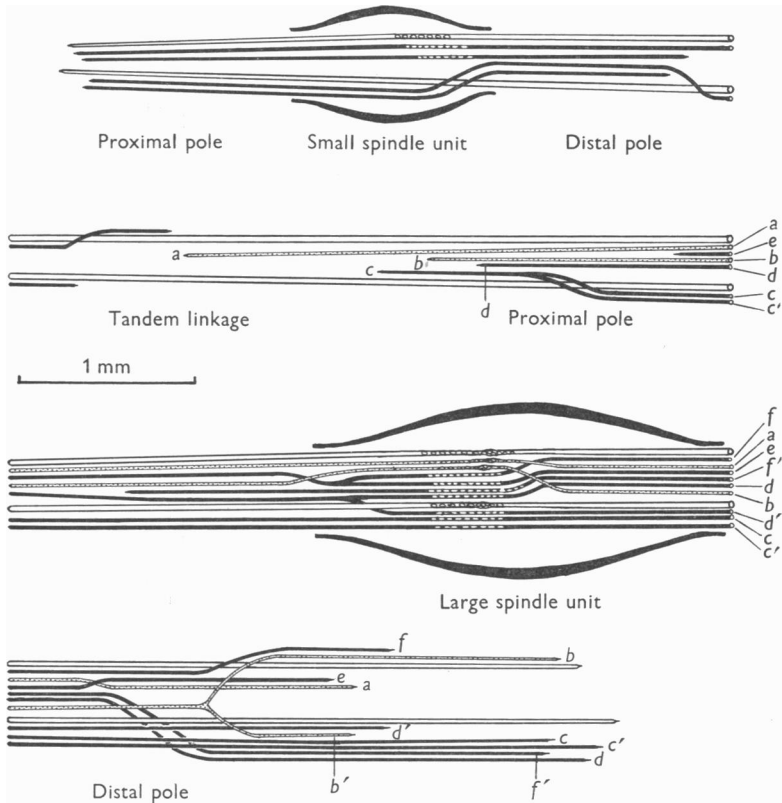
Text-fig. 4. Projection-plan of double tandem spindle from cat rectus femoris shown as if cut into four portions. Large fibres white, intermediate fibres stippled, small fibres black. Scale applies to fibres only; scale for width × 2 that for length, and diameters standardized. Equatorial encapsulations indicated as fusiform swellings; nuclei schematic, but length of each nucleated region accurate. Full description in text. Photographs of the bifurcation of fibre b are shown in Pl. 1.

a few muscle fibres linked, by two large fibres, to a large capsule in which the fibres are more numerous. In the small spindle unit four single small fibres accompany the two continuous large ones; the equatorial nucleation of the fibres is characteristically sparse and comprises three nuclear chains and three fibres in which polar nucleation is retained. In the large spindle unit, the large fibres are accompanied by two intermediate fibres (a and b) and four small (c–f). Fibre a remains single while b

branches in the distal pole to produce a short branch b': it is this bifurca-
tion that is illustrated in Pl. 1. Of the four small fibres, three branch
(c, d, and f), while e remains single: none of the branching fibres reunite.
Owing to differences of fibre length, and to branching, the numbers of
fibres composing the large spindle unit, as counted at one-millimetre
intervals from the proximal polar extremity to mid-equatorial region,
increases in the progression 3, 7, 8, 9, 11. The equatorial nucleation com-
prises four nuclear bag and myotube regions belonging to the large and
intermediate fibres, and seven nuclear chains. The stable position of the
large fibres, and the changes in position of the small and intermediate
fibres, are represented as accurately as possible.

It occasionally happens that a few extrafusal muscle fibres run a parallel
course with a spindle and become enclosed within the capsule together
with the intrafusal bundle. Baum (1900) and Cooper (1960) have made
similar observations. On the rare occasions when this occurs the intra-
fusal and extrafusal fibres are always segregated in separate capsular
compartments. In common with Häggqvist (1960), we have not observed
supplementary bundles of intrafusal muscle fibres joining the spindle by
penetrating the equatorial encapsulation as described by Cilimbaris (1910).

DISCUSSION

The branching of intrafusal muscle fibres has long been a matter of
dispute, partly because of the intrinsic difficulties of demonstrating
it, and partly because of inadequate histological methods employed. For
example, the practice of selecting sections at regular intervals in a
transverse series and discarding the rest is a severe handicap to drawing
any valid conclusion. A fibre branches within the space of a few trans-
verse sections covering 60–90μ, so that gaps in a series of e.g. 85μ (Swett
& Eldred, 1960) are unlikely to reveal the process. Pronouncements
made on the basis of studying serial longitudinal sections and teased gold-
chloride preparations (e.g. Barker, 1948), or methylene blue preparations
(e.g. Gray, 1957), are also of little significance for it is extremely difficult
to trace individual members of the intrafusal bundle with certainty for
any considerable length in such material. Dissociating methods also, in
our experience, give equivocal results. The only adequate approach is to
trace a fair sample of spindles from end to end in a complete series of
transverse sections cut exactly at right-angles to the axis of muscle fibre
orientation. Even in such material the small fibres, in particular, are
often difficult to trace, and the chances of error are greater, for example,
than in tracing nerve fibres of equivalent dimensions. The changes of
diameter, position, and number of fibres in the intrafusal bundle, inter-

mixed with a profusion of nerve fibres and nuclei, often present a complex picture in which several interpretations are possible, and our present position has only been attained gradually, the stringency of criteria and rejection of ambiguities increasing together with sampling and with tracing practice. It is satisfactory to note that our results correspond in many ways to those presented by Boyd (1960). We differ mainly in recognizing an intermediate type of fibre, and in maintaining that branching fibres may reunite. It is possible that the rare branching of nuclear-bag fibres noted by Boyd occurred in fibres that we would classify as intermediate.

While the bimodal distribution of the diameters of intrafusal muscle fibres is now firmly established (see e.g. Walker, 1958; Boyd, 1960; Swett & Eldred, 1960), it is significant that Cuajunco (1927, 1940) recognizes fibres of large, medium, and small size in spindles from adult pig and human biceps brachii. In his earlier study of the pig he gives fibre diameters of 18μ large, 12μ medium, and 6μ small (adult, polar measurements), but in his later human study he records the diameters of large and small fibres only, noting that 'the intermediate group varies between these two extremes' (p. 123). He found that the large fibres were the first to arise in development; that the medium fibres arose from somewhat younger myoblasts grouped with the first; and that the small fibres were added later, either by the splitting of the original cells, or by the incorporation of new myoblasts. It seems probable that the additional intrafusal fibres are recruited from cells surrounding the large fibres in much the same way that the number of extrafusal fibres is generally held to increase in the later stages of development by new fibres arising in the neighbourhood of primary muscle fibres to form 'primary' muscle bundles (see J. D. Boyd, 1960). In fact, if the accounts of Tello (1922) and Cuajunco (1927, 1940) of spindle development are related to knowledge of extrafusal muscle fibre development, we may regard the intrafusal bundle as retaining many of the characteristics of a 'primary' extrafusal bundle in consequence of the retardation of development that follows receipt of the primary afferent innervation. The branching of small and intermediate fibres that occurs in some adult spindles is presumably the result of fibres which, though arising from new cells, nevertheless bifurcate during their subsequent growth. The factors which result in such branching in intrafusal bundles but not, apparently, in extrafusal ones, remain to be elucidated in future accounts of muscle development.

An attempt to relate the innervation of the muscle spindle with the individual fibres in the intrafusal bundle has been made by Boyd (1958, 1959). He maintains that the large muscle fibres are innervated by medium-sized efferents which form discrete end-plates of the typical extrafusal type, while the small muscle fibres are innervated by small efferents,

which form plates that are smaller and more variable in form. He has established the efferent nature of another type of ending which assumes the form of a diffuse and often extensive network; this is also, according to him, located on the small muscle fibres. With regard to the afferent innervation, Boyd maintains that while the primary ending is common to both large and small muscle fibres, the secondary ending is located almost exclusively on the latter. Finally, he distinguishes between (1), 'simple' spindles with muscle fibres similar in diameter innervated by a primary ending and discrete end-plates, and (2), 'compound' spindles in which the small muscle fibres, innervated as he describes, are combined with the large. In this scheme there is thus provision for the two types of efferent behaviour of the spindle, whether these are both attributable to efferent fibres within the γ range (Pascoe, 1958; Boyd, 1959; Boyd & Davey, 1959), or whether fast α fibres (Granit, Pompeiano & Waltmann, 1959) also play a part. It remains to be seen, however, whether further histological work will confirm this analysis. In the mean time the following points suggest that it may be premature to accept it: (i) While large muscle fibres are always present in the intrafusal bundle, many spindles occur in which medium-sized efferents, as judged by intramuscular diameter, play no part in the innervation (M. N. Adal & D. Barker, unpublished). (ii) In rectus femoris spindles, small muscle fibres are always present in the intrafusal bundle, and bimodality of muscle fibre diameter is always evident. (iii) If the properties of fast and slow muscle fibres may be related to their fibrillar and areal pattern in transverse section, as Krüger (1952) maintains, and if the supposition is correct that there are 'twitch' and 'tonic' mechanisms in the spindle, then one might expect the intrafusal muscle bundle to consist of a combination of wholly fibrillar and areal fibres, but this is not so. Each fibre is both areal and fibrillar in varying proportions, but always predominantly fibrillar. Moreover, the application of Krüger's theory of mammalian muscle does not agree with physiological evidence (see Hunt & Kuffler, 1951), and Eyzaguirre (1960) has failed to detect intrafusal responses in the cat which had the characteristics of slow fibres. (iv) The supposition that nuclear-bag and nuclear-chain fibres constitute separate functional systems must take account of the fact that a nuclear-bag fibre of the intermediate type may bifurcate to produce a nuclear-chain fibre as a side branch. (v) The location of secondary endings almost exclusively on small muscle fibres is doubted by Barker & Ip (1961) in their study of single and tandem spindles in the cat. (vi) Boyd's innervation analysis was made on gold-chloride and methylene blue preparations. In our experience, it is doubtful whether such material is adequate to permit the relation of spindle nerve endings to individual muscle fibres with certainty. We believe

that this information may best come from tracing a number of silver-impregnated spindles in serial transverse section, and this work is in progress.

SUMMARY

1. The morphology of the intrafusal muscle fibre in the cat was studied mainly in serial transverse sections, the most detailed information being derived from graphic reconstructions of thirty-two spindles. The muscle most frequently used was rectus femoris.

2. The intrafusal bundle of single spindles and tandem spindle units consists of four to twelve muscle fibres of which both length and diameter measurements are bimodal.

3. Large, intermediate, and small types of intrafusal muscle fibres are recognized. The large fibres possess nuclear-bag and myotube regions, and are the longest; they do not branch. Their diameter (12–26μ), and their position in the intrafusal bundle, undergo little change. The intermediate fibres resemble the large but they occasionally branch. Their position tends to change in the intrafusal bundle and their diameter (10–16μ) undergoes considerable variation. The small fibres have a diameter of 4–12μ and possess nuclear chains in the equatorial region. About one in five branches, and their position in the intrafusal bundle undergoes frequent change.

4. From one to three large fibres (usually two), and from one to eight small fibres (usually four or five) were present in all spindles; intermediate fibres (usually one, occasionally two) were present in about one third.

5. The branching of a small or intermediate fibre takes place over a distance of 60–90μ. With one exception, this always occurred in the proximal pole or in the proximal part of the equatorial region. The two fibres produced may either taper off, or reunite in the distal pole or distal part of the equatorial region. The process of branching or reuniting is quite distinct from the condition where one fibre tapers off alongside another; tapering usually occupies a length of several hundred microns.

6. In the spindles studied all the muscle fibres were predominantly fibrillar, the areal structure occupying a minor proportion of their total length and being most typically present in the juxta-equatorial regions.

7. Reasons are given which suggest that it may be premature to accept Boyd's analysis (1958, 1959) of the innervation of the spindle in terms of the individual muscle fibres composing it.

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EXPLANATION OF PLATES

PLATE 1

Bifurcation of fibre *b* belonging to the double tandem spindle from cat rectus femoris shown in projection-plan in Text-fig. 4. Figs. 1 and 12 are camera-lucida outline drawings in which the large fibres are indicated by L, and the other fibres are lettered as in Text-fig. 4. Serial transverse 12μ paraffin sections stained with haematoxylin and eosin; there is an interval of 3 sections between figs. 1 and 2, and between 4 and 5; 5 sections between figs. 3 and 4; and 6 sections between figs. 2 and 3. Figs. 5–12 represent serial sections. In fig. 9 a crack is present in the bifurcating fibre *b* as an artifact just above the region of constriction. Note (i) fluctuation in diameter of the intermediate fibre *a*; (ii) fibrillar pattern of, e.g. fibres *a* and *b* as compared with areal pattern of, e.g. fibres *d′* and *f′*; (iii) change in structural pattern of fibre *d* from areal in fig. 2 to fibrillar in fig. 11.

PLATE 2

Figs. 1–9. Bifurcation of fibre A belonging to the single spindle from cat rectus femoris shown in Text-fig. 2. Figs. 1 and 9 are camera-lucida outline drawings of the sections illustrated in figs. 2 and 8 respectively, and the fibres are lettered and numbered as in Text-fig. 2. Serial transverse 12μ paraffin sections stained with haematoxylin and eosin; there is an interval of 6 sections between figs. 2 and 3; 2 sections between figs. 4 and 5; 75 sections between figs. 5 and 6; 8 sections between figs. 6 and 7; and 38 sections between figs. 7 and 8. Figs. 3 and 4 represent adjacent sections. Note (i) equatorial nucleation of fibres L, *a*, and *a′* in figs. 6 and 7; (ii) narrower width of the intrafusal bundle and the fibres composing it in fig. 6; (iii) areal pattern of fibre L in fig. 2 as compared with its fibrillar pattern in fig. 8.

Figs. 10–13. Tapering of a fibre *t* alongside a longer fibre which does not alter in diameter. Sections and staining as above; there are successive intervals of $336\,\mu$, 120μ, and 60μ respectively between figs. 10 and 11, 11 and 12, and 12 and 13. Proximal pole of single spindle from cat rectus femoris.

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