THE NUMBER AND DISTRIBUTION OF MUSCLE-SPINDLES IN CERTAIN MUSCLES OF THE CAT

By D. BARKER AND N. K. CHIN

Department of Zoology, University of Hong Kong

As a preliminary to quantitative studies of the proprioceptive equipment of various muscles in the cat, it became necessary to determine whether there was any correlation between the number of muscle-spindles contained in a given muscle and in its partner on the opposite side of the animal. Such a correlation might be expected as part of the expression of the bilateral symmetry of the animal. Although Morpurgo (1897) reported eight spindles in each sartorius muscle of the rat, Tower (1932), in a study of the interosseous muscles of the cat's forelimb, counted twenty-two spindles in the left Vth interosseus as compared with fourteen in the right, and concluded that there was little correspondence between the spindle content of identical muscles on opposite sides of the same individual. Apart from these observations the literature lacks any reference to paired counts of spindles (i.e. counts of the spindle content of a pair of identical muscles from the same animal). Those who have pursued such quantitative studies in the past (e.g. Gregor, 1904; Voss, 1937) have been primarily concerned with determining the spindle content of individual muscles and devising different methods of expressing 'spindle density', i.e. the proportion of the spindle content to the weight or volume of the muscle, or the proportion of the total length of the spindles counted to the weight of the muscle, and so on.

If it were to be established that a close and predictable correlation exists between the number of spindles in a given muscle and its partner, it would clearly be a considerable asset in histological and physiological investigations of this proprioceptor. It was obvious that if a result of significance was to emerge it would have to be based upon many paired counts, and from the outset we attached little importance to Morpurgo's observation or to Tower's conclusion that there was no correlation since each of these was based on only one such count.

A natural extension to the work of counting the number of spindles in a muscle is simultaneously to record their distribution within it. The large number of counts made in the limb muscles used afforded an opportunity for obtaining information about their spindle distribution to an extent which has so far only been achieved for the extraocular muscles (see Cooper & Daniel, 1949; Merrillees, Sunderland & Hayhow, 1950; Cooper, Daniel & Whitteridge, 1955).

MATERIALS AND METHODS

The muscles investigated were the rectus femoris, tibialis anticus, and Vth interosseus (forelimb) of the cat. Twenty paired counts were made of each muscle, the sex of the animals used being kept in equal proportions and litter-mates being

avoided. In order to reduce the quantity of sections, the muscles were usually obtained from 0 to 21-day-old kittens, though two pairs of rectus femoris and seven pairs of Vth interosseus were obtained from adults. The muscles were fixed in a stretched condition, the entire limb being placed in Bouin's fluid, and were subsequently dissected out in 70 % alcohol. The counts were made from serial horizontal longitudinal paraffin sections cut at 10μ and stained with haemotoxylin and eosin. Some muscles were stained using the Holmes silver technique in order to study the nerve-entry and distribution of intramuscular nerve trunks.

In making the spindle counts, each section of the series was examined and the position of each spindle was noted in terms of the micrometer scale readings of the microscope's mechanical stage, the nuclear bag region being taken as the measuring point. All the counts were checked by re-counting a second time, and in some cases a third time: one third of the counts were further checked by our colleague Mr M. C. Ip.

The first muscle studied was rectus femoris. This is a pinnate muscle with a centrally placed tendon running in a sagittal plane through most of its length. The position of each spindle counted in this muscle was originally recorded in terms of the distance of its nuclear bag region from the central tendon and from the proximal and distal ends of the muscle, a method later discarded on the acquirement of a Shadowgraph contour projector. Using this apparatus a tracing was made of the projected image of every fifth section of a series, the position of the spindles being marked in directly on each tracing. This method rendered it possible to represent the distribution of spindles within any given muscle as follows: (a) by preparing histograms plotting spindle number against muscle length, muscle width (rectus femoris only), and muscle depth; (b) by preparing a projection-plan of the muscle in which the positions of all spindles present are charted within the limits of a tracing of a single representative horizontal longitudinal section.

RESULTS

Number of muscle-spindles

The results of the twenty paired counts for each muscle are shown in Table 1 and are represented graphically in Fig. 1. They provide information about the variation of the spindle content of a given muscle, and the nature of the difference in spindle content between members of a pair.

With regard to spindle content, the lowest count in rectus femoris was 77 and the highest 132, giving a range of 56 for the 40 muscles counted and a mean spindle content of $104 \cdot 15 \pm 13 \cdot 55$ (S.D.). In tibialis anticus the lowest count was 52 and the highest 89, a range of 38, and the mean content was $70 \cdot 65 \pm 8 \cdot 76$ (S.D.). In Vth interosseus (forelimb) the lowest count was 21 and the highest 31, a range of 11, and mean content of $25 \cdot 1 \pm 2 \cdot 36$ (S.D.). Though Tower (1932) also found a range of 11 for this muscle, the 10 counts made fell between 14 and 24, with a mean content of 19. We are inclined to attribute the discrepancy between these results and our own to the possibility that Tower failed to count the complete spindle content in her Bielschowsky preparations. Our own results are based on the thoroughly checked counts of 40 Vth interossei and were made with the experience of having

previously counted and re-counted the spindle contents of 20 pairs of rectus femoris and tibialis anticus muscles.

The limits of difference in spindle content between members of pairs were from 1 to 9 in rectus femoris, with a mean difference of 4·4; from 1 to 8 in tibialis anticus, with a mean of 3·8; and from 0 to 4 in Vth interosseus with a mean of 2·2 (see Fig 2). We would discount Tower's difference of 8 in her one paired count of Vth interosseus (14 as to 22) for the reasons already given. The correlation coefficient (r) of the paired counts of rectus femoris is 0·94, of tibialis anticus 0·87, and Vth interosseus 0·41. The comparatively low value of r for Vth interosseus is due to the fact that
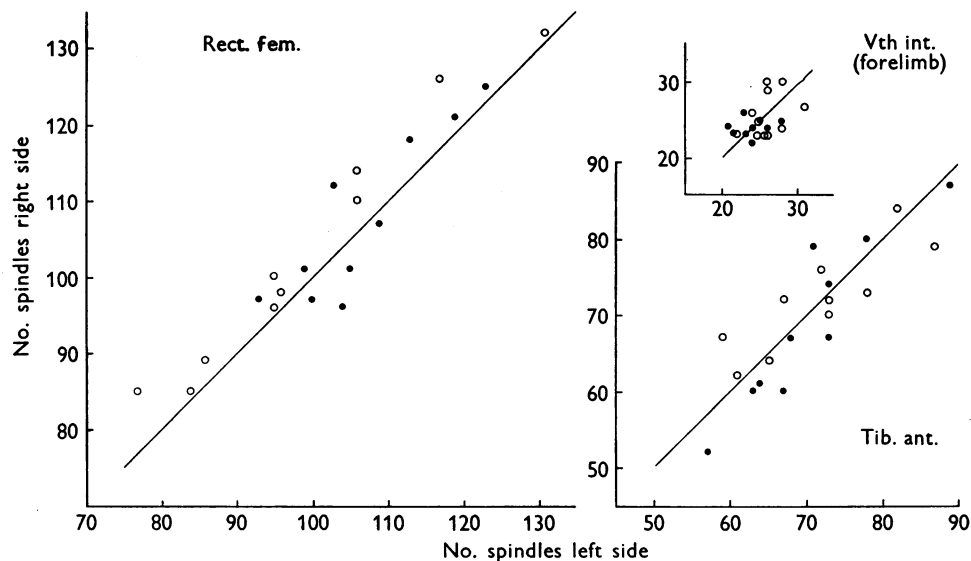

Fig. 1. Graphic representation of the spindle contents of rectus femoris, tibialis anticus, and Vth interosseus (forelimb) of cat as determined by 20 paired counts of each muscle. Each circle represents one paired count; hollow circles, females; black circles, males. Line between points shows where points would lie representing members of a pair of muscles with identical spindle content.

although the limit of difference between each member of a pair is four spindles, and thus lower than that of the other muscles, it is by contrast a significant fraction of the spindle content. Thus while a close equivalence in spindle content between pairs of muscles containing few spindles is to be expected on functional grounds, the level of significance in terms of r is inevitably poor. An extreme case is provided by the frog toe muscle containing only one spindle from which Matthews (1931) recorded in his first single-fibre experiments. Paired counts of this muscle might well reveal the occasional presence of two or three spindles, and while this would be functionally acceptable, the value for r would be virtually zero.

Bearing in mind that the main objective of these counts was to ascertain whether the spindle content of one member of a pair of identical muscles could be predicted if the content of the other member was known, the results as they stand reveal no more than the range of difference between pairs as established by 20 paired

Table 1. *Paired counts of the number of muscle-spindles in three limb muscles of the cat*

C = adult cat; K = 0 to 21-day-old kitten; R.D. = range of difference.

Sex	Rectus femoris				Tibialis anticus				Vth Interosseus (forelimb)			
	Ref. no.	Left	Right	Difference, right as to left	Ref. no.	Left	Right	Difference, right as to left	Ref. no.	Left	Right	Difference, right as to left
Female	C4	95	96	+1	K17	61	62	+1	C23	22	23	+1
	C9	77	85	+8	K24	82	84	+2	C22	26	30	+4
	K11	117	126	+9	K28	67	72	+5	C26	26	28	+2
	K19	106	114	+8	K62	73	70	-3	C28	28	24	-4
	K30	106	110	+4	K69	78	73	-5	C33	26	29	+3
	K38	86	89	+3	K71	87	79	-8	C35	28	30	+2
	K45	95	100	+5	K73	73	72	-1	K51	31	27	-4
	K49	84	85	+1	K76	59	67	+8	K54	24	26	+2
	K51	131	132	+1	K79	72	76	+4	K62	25	23	-2
	K54	96	98	+2	K82	65	64	-1	K69	26	23	-3
Totals		993	1035	+9 to +1		717	719	+8 to -8		262	258	+4 to -4
Male	K6	123	125	+2	K14	73	67	-6	C25	28	25	-3
	K9	100	97	-3	K25	57	52	-5	K52	25	25	0
	K10	119	121	+2	K43	67	60	-7	K60	22	23	+1
	K12	113	118	+5	K44	64	61	-3	K63	21	24	+3
	K25	105	101	-4	K56	68	67	-1	K73	23	26	+3
	K34	94	101	+7	K58	89	87	-2	K74	24	24	0
	K35	93	97	+4	K60	63	60	-3	K75	23	25	+2
	K41	104	96	-8	K65	73	74	+1	K77	25	25	0
	K43	109	107	-2	K67	78	80	+2	K81	24	22	-2
	K57	103	112	+9	K77	71	79	+8	K83	26	24	-2
Totals		1063	1075	+9 to -8, R.D. = ±9		703	687	+8 to -7, R.D. = ±8		241	243	+3 to -3, R.D. = ±4
		2056	2110			1420	1406			503	501	
Mean spindle content and S.D.		104.15±18.55				70.65±8.76				25.1±2.36		
Spindle content range		77 ↔ 132 = 56				52 ↔ 89 = 38				21 ↔ 31 = 11		
Mean difference between pairs		4.4				3.8				2.2		

counts. Thus if the number of spindles in the tibialis anticus muscle on one side of a cat is counted we may presume that the muscle on the other side will at the most have either eight more or eight less spindles than its partner. But the difference might well be much less, for the mean difference is 3·8 and 55 % of the pairs differed by 3 or less. We have therefore used the data obtained in deriving r and applied the regression line equation in order to obtain the best estimate of the spindle content of the left-hand muscle (y) when the spindle content of the right-hand
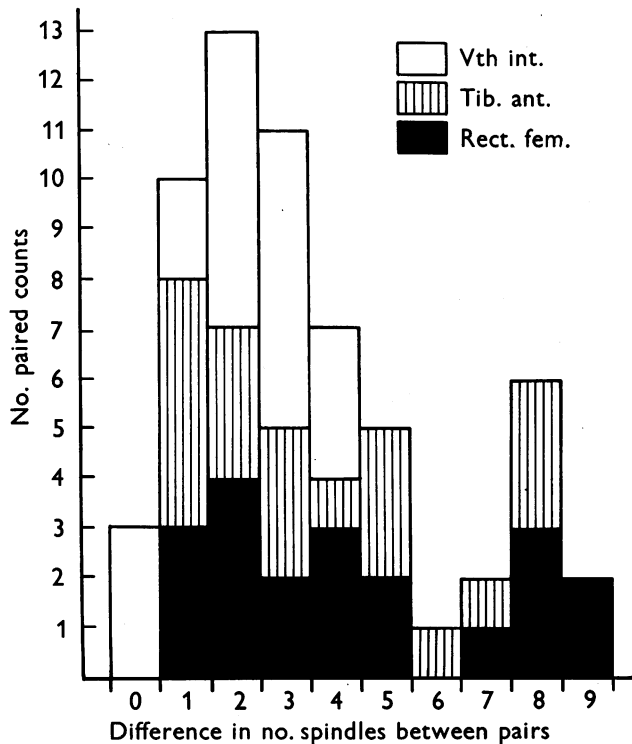

Fig. 2. Distribution of the differences in spindle content between members of pairs
of the three cat muscles studied.

muscle (x) is known, and vice versa. Thus the best estimate of y from a known value of x for rectus femoris is $4·7 + 0·93x$; for tibialis anticus, $12·0 + 0·84x$; and for Vth interosseus (forelimb), $14·4 + 0·43x$. Similarly, the best estimate of x for a known value of y for rectus femoris is $6·8 + 0·96y$; for tibialis anticus, $7·1 + 0·89y$; and for Vth interosseus, $14·0 + 0·4y$.

Within the limits of the study made, these results show that there is a close correlation between the spindle content of a pair of identical muscles from one individual. Of the total of 60 paired counts made of the three muscles studied, the difference in the spindle content of a pair ranged from 0 to 9 (Fig. 2). In three pairs of muscles (all Vth interosseus) the spindle content of each side was identical; in 24 pairs the left muscle had a greater spindle content than the right, as against 33 pairs in which the right had a greater spindle content than the left. There is thus

a tendency towards asymmetry, but it is doubtful whether our relatively small sample can be regarded as a significant anatomical expression of the frequency of use of right and left limbs. We are on firmer ground in concluding that in muscles such as those we have studied, the lower the spindle content (a) the narrower is the range of spindle content (56, 38, and 11 in this series for muscles of mean spindle content of $104\cdot15 \pm 13\cdot55$, $70\cdot65 \pm 8\cdot76$, and $25\cdot1 \pm 2\cdot36$); and (b) the closer is the equivalence in content between members of a pair (mean differences of $4\cdot4$, $3\cdot8$, and $2\cdot2$, and ranges of difference of ±9, ±8, and ±4 in this series). Thus, for example, we would expect a muscle with a mean spindle content of 50 to vary in spindle content over a range of the order of 25, to have a mean difference of the order of 3 in spindle content between pairs, and a range of difference of the order of ±6. We can say little about muscles with a spindle content considerably greater than rectus femoris beyond suggesting that it is unlikely that range and difference increase in a linear fashion, and pointing out that human error would play an increasing part in the high counts that would have to be made.

Distribution of muscle-spindles

It has been frequently stated that the greatest number of spindles in a muscle occurs in its 'belly' or in the 'region of nerve-entry'. Gregor (1904) indicates nerve-entry points on his graphs of spindle number plotted against muscle length (human foetal material), but apart from this, and early work on whole mounts of muscle (e.g. Kölliker, 1862; Mays, 1884) and studies of extraocular muscles (e.g. Cooper & Daniel, 1949), no attempts have been made to correlate the distribution of spindles in a muscle with the entry and distribution of its nerve supply. Clearly the two distributions must coincide to a large extent for there is generally little intramuscular segregation of motor and sensory nerve fibres. However, the fact remains that portions of muscle taken from nerve-entry or belly regions often have a low spindle content indicating that the matter requires further elucidation. We have endeavoured to do this by preparing projection-plans of each of the muscles studied showing the distribution of the spindles and nerve supply and relating these to histograms of the spindle content in terms of muscle length, width (rectus femoris only), and depth.

Rectus femoris. This is the central muscle of the quadriceps group taking its origin from the anterior border of the acetabulum and ventral border of the ilium, and inserting on to the proximal border of the patella. The tendon of origin is prolonged within the body of the muscle in the sagittal plane as a central tendon, which terminates in the distal sixth of the muscle. An aponeurosis envelops the entire muscle, increasing in thickness towards the distal end particularly on the ventral and medial sides. A small slip of muscle is located on the medial side at approximately one-third of the distance from origin to insertion: it consists of a small group of muscle-fibres segregated from the rest by a short intramuscular tendon connected with the aponeurosis, and possibly represents the posterior head of the muscle as found in the rat. The belly of the muscle is oval in cross-section but the muscle flattens out dorso-ventrally towards each end. The muscle-fibres are arranged for the most part in a pinnate fashion and the bulk of them take their origin from the central tendon and insert on to the enveloping aponeurosis.

These features are shown schematically in Fig. 3 A with the addition of the entry and distribution of the nerve supply and the distribution of the spindles. The muscle is innervated by a branch of the femoral nerve, which splits into two branches (*a* and *b*) prior to entering the muscle medially, ventrally, and obliquely in the proximal quarter just above the region of the slip. In adult cats branch *b* often enters more
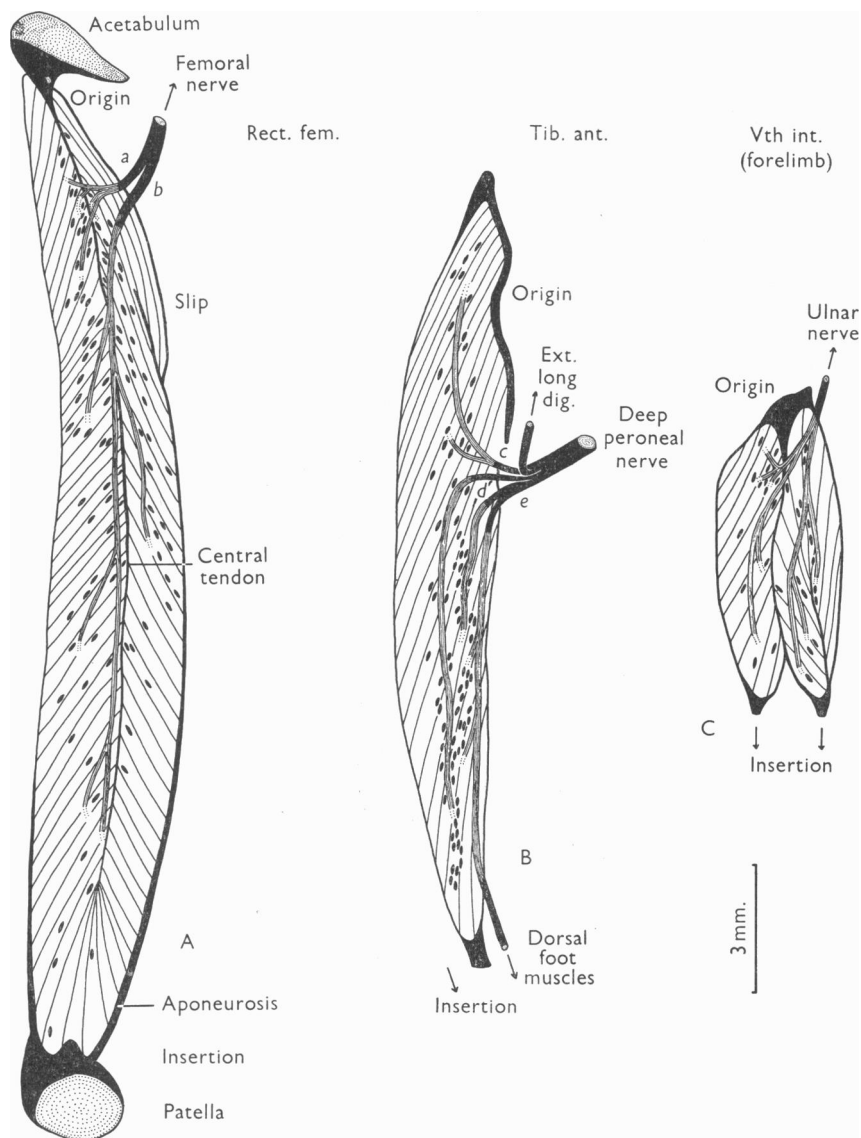

Fig. 3. Projection plans of cat rectus femoris (A), tibialis anticus (B), and Vth interosseus of forelimb (C) showing distribution of spindle and nerve supply. Spindles shown as black oval symbols; nerve branches *a–e* (see text) shown black up to point of entry into muscle. Based on data from right rectus femoris of kitten, K 54; right tibialis anticus of kitten K 79; and right Vth interosseus (forelimb) of young cat C 22.

distally, either in the region of the slip or just below it. The smaller and proximal branch *a* splits up into four major intramuscular trunks innervating the proximal third of the muscle: three of these trunks penetrate the central tendon to subdivide further on the lateral side. The larger branch *b* approaches the central tendon, which it penetrates after leaving one trunk on the medial side: the remaining trunks, four in number, all supply the lateral side. Branch *b* thus supplies the middle and distal thirds of the muscle. This pattern, with minor variations, held for all muscles studied. The most common variation was for the medial trunk of branch *b* to split off earlier than shown in Fig. 3A, in a few cases even prior to nerve-entry. In every distribution, however, the largest number of nerve trunks was to be found on the lateral side of the muscle.

It is clear from the distribution of the spindles as shown in Fig. 3A that the majority is located in the lateral half of the muscle. In this particular animal (K 54) there were 58 spindles in the lateral half as compared with 40 in the medial half. To a greater or lesser extent this is always the case, but more pronounced features are the concentration of spindles in the ventral half of the muscle and the preponderance of spindles in the proximal as compared with the distal half of the muscle. Histograms of the spindle distribution emphasize these features, and when the histograms for each member of a pair of recti from one individual are compared there is seen to be a close similarity in distribution on the two sides (see Fig. 4). A comparison of histograms prepared of the spindle distribution in six pairs of recti suggests that only minor variations occur between different individuals. If the muscle length histograms for rectus femoris in Fig. 4 are compared with the spindle-number muscle-length graph prepared by Gregor (1904, fig. 18) for the rectus femoris of a human foetus, it is clear that in both cat and man the majority of the spindles in this muscle lies in its proximal half. The nerve-entry points on Gregor's graph, and his text, also suggest that the nerve entry and supply of the muscle are similar. The comparison is somewhat marred by the fact that Gregor did not examine that part of the muscle corresponding to the proximal third of the femur.

We may summarize these results as follows. The nerve supply of the rectus femoris muscle of the cat enters the proximal quarter of the muscle on the ventro-medial side and is distributed intramuscularly primarily on the ventro-lateral side. The spindles are distributed in greater quantity in the ventral half of the muscle than the dorsal, more in the proximal half than the distal, and more in the lateral half than the medial. The greatest concentration of spindles occurs in the proximal ventro-lateral eighth of the muscle.

Tibialis anticus. This muscle lies superficially on the lateral side of the shank, its inner concave surface clothing the underlying extensor longus digitorum. Its origin from tibia and fibula extends for about one-third of its length on the medial side, and its insertion is by way of a long tendon, which ultimately attaches on to the outer surface of the first metatarsal. The muscle fibres run diagonally and medio-laterally as shown in Fig. 3B. The innervation is supplied by the deep peroneal nerve, which enters the muscle on the medial side in the middle third region with respect to depth, and approximately at the junction of the proximal and middle third regions with respect to length. Prior to entering the muscle, the nerve divides into four branches, three of which enter the tibialis anticus (*c*, *d*, *e*), while the fourth

innervates the extensor longus digitorum (see Fig. 3B). The proximal third of the muscle is innervated by branch *c*, the rest by *d* and *e*; branch *e* splits into two intra-muscular trunks, the most medial of which, after contributing to the innervation of
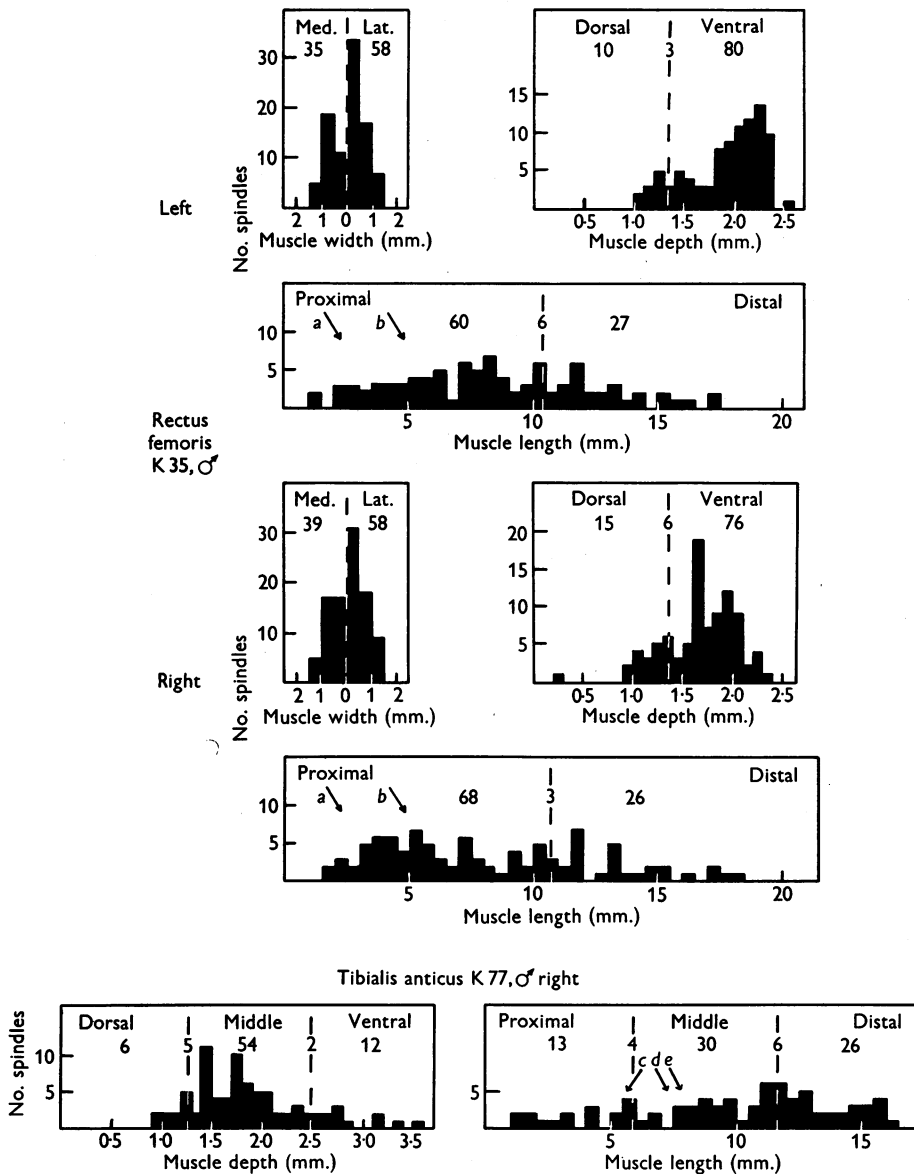

Fig. 4. Distribution of spindles in cat rectus femoris and tibialis anticus muscles as illustrated by histograms plotting spindle number against muscle width (rect. fem. only), depth and length. The distribution is shown for one pair of recti from kitten K 35, and for the right tib. ant. from kitten K 77. *a*, *b*: proximal and distal branches of nerve supplying rect. fem. (cf. fig. 3A); *c*, *d*, *e*: nerve branches supplying tib. ant. (cf. fig. 3B). Arrows indicate nerve-entry points (tips of arrows) and direction of entry (angle of arrows).

tibialis anticus, emerges at the distal end of the muscle with the tibialis artery to travel to the foot, where it innervates the dorsal muscles.

The distribution of spindles is shown in Fig. 3B, a projection-plan of the muscle from the right side of kitten K 79, and in Fig. 4, which illustrates the distribution in the right-hand muscle of kitten K 77 by means of histograms in terms of muscle depth and length. The spindles are seen to be distributed in the neighbourhood of the intramuscular nerve trunks, the greatest concentrations being in the middle third of the muscle with respect to depth (i.e. the level of nerve-entry) and in the middle and distal thirds with respect to length. The portion of the muscle containing the least number of spindles is the dorsal and proximal ninth. A comparison of our muscle-length histograms with the spindle-number/muscle-length graphs prepared by Gregor (1904, figs. 34, 35) for the human foetal tibialis anticus, suggests a similar spindle distribution in this respect in both cat and man.

Vth interosseus (forelimb). This is a small stout muscle lying on the palmar surface of the fifth digit of the paw. It is double-bellied and has a single origin, two tendons of insertion, and a pinnate arrangement of muscle fibres (see Fig. 3C). The innervation is supplied by the deep palmar branch of the ulnar nerve, which enters the muscle from the medial side at the proximal end at the level of the middle third region with respect to depth. After entry the nerve branches into two intramuscular trunks, which supply the medial and lateral halves of the muscle. As in the other muscles described, the spindles are distributed in the neighbourhood of the intramuscular nerve trunks. Histograms of the distribution show that most of the spindles are located in the proximal and middle thirds of the muscle with respect to length, and the middle and ventral thirds with respect to depth.

DISCUSSION

The fact that the spindle contents of a pair of identical muscles from one individual are closely equivalent is not an unexpected finding, but the demonstration in the muscles studied that this is so, together with the establishment of the limits of difference and prediction of difference formulae have useful applications, of which we are already taking advantage in other work. It may eventually be possible from the result of a single count of any given muscle, to predict its range and mean spindle content, and range and mean difference between members of pairs, but the data from a large quantity of paired counts of many muscles would be necessary before this could be realized. Hines & Tower (1928) were of the opinion that the number of spindles in a given muscle was approximately constant, but it has been clear for some time that the spindle content does in fact vary in different individuals (see, for example, the results of Voss, 1937, for human lumbricales muscles; and Merrillees *et al.* 1950, for the human superior oblique muscle). It is also evident that the spindle content of a muscle does not necessarily bear any relation to its size. That the spindle content of a muscle varies is, however, sometimes ignored. Thus, for example, Hagbarth & Wohlfart (1952) relate a spindle count of 57 for the tibialis anticus muscle of one cat with the afferent fibre diameter spectrum of another on the assumption that the spindle content of the muscle in both cats was the same. Their deductions are accepted by Granit (1955) but the basis for them is clearly

invalid; as our results show, the spindle content of the muscle in the operated cat could have been anything between 52 and 89, the probability being 67·5 % that it lay between 62 and 79.

The use of kitten muscles for a large number of the counts might be objected to in view of the possibility of a post-natal increase in the number of spindles. However, studies of the development of spindles (e.g. Tello, 1917; Cuajunco, 1927) make it clear that the spindle content of a muscle is established before birth and that post-natal morphogenesis is simply concerned with further changes (increase in length, elaboration of capsule, etc.) in spindles already present (Kalugina, 1956; Zelená, 1957). Voss (1937) found no significant increase in the spindle content of the lumbricales muscles of the human hand in counts made on newly-born and adult material, and this is also our experience in counts of kitten as compared with adult muscles (rectus femoris and Vth interosseus, forelimb).

Our counts of spindles were made on the assumption that the receptors consisted of a single encapsulated region situated equatorially between two poles in accordance with the classical descriptions. However, Cooper & Daniel (1956) have described the occurrence of 'tandem' spindles in human hand and neck muscles in which several capsular regions occur successively in series, and Gray (1957) has described similar 'spindle systems' in the ext. long. dig. IV muscle of the frog. Tandem spindles with two, and occasionally three, successive capsular regions have been observed by Barker and Ip (unpublished) in the rectus femoris muscle of the cat and their results at present suggest that about 20 % of the spindles in this muscle are of this type. In longitudinal sections, as used in this study, it is impossible to decide whether or not two or three closely associated capsular regions belong to separate spindles or to one tandem spindle. In view of these observations, our counts of spindles should more accurately be regarded as counts of encapsulated sensory regions of spindles, a proportion of which are arranged in tandem.

Previous studies of spindle distribution have been made almost exclusively on muscles cut in serial transverse section. This permits variations in spindle length to be recorded and providing that due attention is paid to the location of each spindle within the muscle, projection-plans of spindle distribution can be prepared. These vary in their usefulness from the clear presentations of Merrillees *et al.* (1950) to the misleading figures of Hagbarth & Wohlfart (1952), which show the distribution of spindles not, as claimed, within the muscle containing them, but simply on the grid used by the authors to record them. While nerve-entry and distribution could be mapped from a transverse section study it would be a laborious undertaking and has not been attempted in the studies made. To this limitation of the method must be added the fact that it can only work well with muscles whose fibres are orientated parallel with the longitudinal axis. By contrast longitudinal sections allow for projection-plans to be prepared, which show muscle-fibre direction, distribution and orientation of spindles, and the entry and distribution of the nerve supply. Moreover, counting, which necessarily goes hand in hand with distribution, is more rapid with spindles cut in longitudinal than in transverse section.

Our distribution results show clearly that in the muscles studied the spindles are distributed in the neighbourhood of the major intramuscular nerve trunks. The same conclusion was drawn by Gregor (1904) in his monumental study of

the number and distribution of spindles in 51 muscles of the human foetus. The pattern of the intramuscular nerve supply of a given muscle is fairly constant, minor variations occurring in different individuals but to an insignificant extent between members of a pair of identical muscles from the same individual. Spindle distribution follows accordingly, so that its pattern in each member of a pair of muscles from one individual is very similar, as Morpurgo (1897) observed in the rat's sartorius. However, since the distribution of major intramuscular nerve trunks follows a different pattern in different muscles, concentrations of spindles do not necessarily occur in 'regions of nerve-entry' or in the 'belly' of a muscle as has often been stated. 'Nerve-entry' concentrations are likely to occur only where there is a rapid subdivision of the intramuscular supply in this region, and 'belly' concentrations only where there is a supply of one or more intramuscular trunks to this region. This feature follows naturally from the manner in which spindles are formed in embryo muscle. It would appear from Tello (1917) that the pattern of the intramuscular nerve supply is established mainly by the extrafusal motor fibres. Spindle formation is initiated when a primary nerve fibre leaves an intramuscular nerve trunk and comes into association with a bundle of myotubes nearby. The characteristic spindle nerve trunks are formed when other nerve fibres destined for the spindle (intrafusal motor fibres, 'accessory' fibres, and in some cases secondary fibres) arrive later and follow the pathway laid down by the primary fibre. Thus providing the primary fibres are distributed generally throughout the intramuscular nerve supply, the distribution of spindles in the neighbourhood of the major intramuscular nerve trunks is bound to follow. With most muscles this would appear to be so but the extraocular muscles are exceptional in that there is a high degree of segregation of the extrafusal motor and spindle supply in the intramuscular trunks, the former being restricted to approximately the middle third of the muscles and the latter either mainly to the proximal third (Cooper & Daniel, 1949, human inferior rectus) or to both proximal and distal thirds of the muscles (Merrillees, *et al.* 1950, human medial and superior recti, and superior oblique).

SUMMARY

A study of the number and distribution of muscle-spindles in twenty pairs each of mm. rectus femoris, tibialis anticus, and Vth interosseus (forelimb) of the cat has shown that:

1. The spindle content of a muscle varies in different individuals, as has been established by other workers. In the 40 counts made of each muscle the spindle content fell between 77 and 132 in rectus femoris (range 56: mean $104 \cdot 15 \pm 13 \cdot 55$ s.d.); 52 and 89 in tibialis anticus (range 38: mean $70 \cdot 65 \pm 8 \cdot 76$ s.d.); and 21 and 31 in Vth interosseus (range 11: mean $25 \cdot 1 \pm 2 \cdot 36$ s.d.).

2. There is a close correlation between the number of spindles in a given muscle and its partner on the opposite side of the animal. In this series the difference in spindle content of a pair ranged from nil to 9. From a statistical treatment of the results, formulae are derived for obtaining the best estimate of the spindle content of the left member of a pair when the content of the right member is known, and vice versa.

3. In these muscles the lower the spindle content, the closer was the equivalence in content between members of a pair (mean differences of 4·4, 3·8, and 2·2, and ranges of differences of ±9, ±8, and ±4 for rect. fem., tib. ant., and Vth int. respectively).

4. Of the 60 paired counts made, the spindle contents of three pairs (all Vth interosseus) were identical, and the right muscle had a higher spindle content than the left in nine more pairs than vice versa.

5. Since it is probable that some of the spindles counted were of the tandem type, our counts should be regarded as counts of encapsulated sensory regions of spindles, a proportion of which are arranged in tandem.

6. Projection-plans of each muscle studied have been prepared showing muscle-fibre direction, distribution and orientation of spindles, and the entry and distribution of the nerve supply. The spindle distribution is also illustrated by histograms of the spindle content in terms of muscle length, width (rect. fem. only), and depth. It is demonstrated that the spindles in a muscle are distributed in the neighbourhood of the major intramuscular nerve trunks. Since the distribution of these trunks follows a different pattern in different muscles, concentrations of spindles do not necessarily occur in 'regions of nerve-entry' or in the 'belly' of a muscle as has often been stated.

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