

CHAPTER II

The Sensory Innervation of Muscles and Tendons

A schematic summary of both the motor and sensory innervation of the muscles is given in Fig. 20 which deserves close study. Its details will be discussed under separate headings, the extra- and intrafusal motor innervation having already been dealt with.

THE MUSCLE SPINDLE

General Description

The terminals of the muscle spindle afferents end on the intrafusal fibres, described in the previous chapter. The largest sensory afferents from muscles were found by Sherrington (1894) to derive from the annulo-spiral terminals encircling the nuclear bag. The term annulo-spiral is Ruffini's (1891, 1897, 1898-99) but nowadays his alternative term "primary endings" or "primaries" is the one used, following a suggestion by Barker (1948) who pointed out that Ruffini's "secondaries" or "flower-spray" endings do not necessarily differ from the primaries except in location (see for example Boyd, 1962). In 1948 Barker's main work was based on rabbit spindles from hindlimb muscles in which ~~there are only~~ nuclear bag intrafusal ~~fibres (as checked by~~ ~~Barker & Hunt, 1964)~~ and in them the secondaries are coiling around the long myotube region in which the aggregate of nuclei is thinning out into a single row. This made me (Granit, 1955a) call them "myotube endings", a term apparently adequate only for the special case of spindles with pure bag intrafusal fibres. This is, nevertheless, an important case because in the rabbit at least, gamma plates and gamma trails apparently coexist on the same bag intrafusal fibre (Adal & Barker, 1965b) and so each of them would be likely to have an effect on its two types of sensory ending. Barker (1948) gave a very good description of the secondaries (silver and gold chloride preparations) and pointed out that their afferent nerves tended to be thinner ($6-9 \mu$) than those of the primaries ($8-12 \mu$), an observation since confirmed by many authors.

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Ruffini, working on cat spindles, classified them on the basis of their dual sensory innervation (he was uncertain as to what the plate endings really were) and the feasibility of this classification was supported by Barker. It is based on the relative number of primaries (P) and secondaries (S). The *simple* organ with P alone is often found in spindles with short intrafusal fibres, for instance at the end of lumbricals and neck muscles in man (Cooper & Daniel, 1963); *intermediates*, P plus S, about

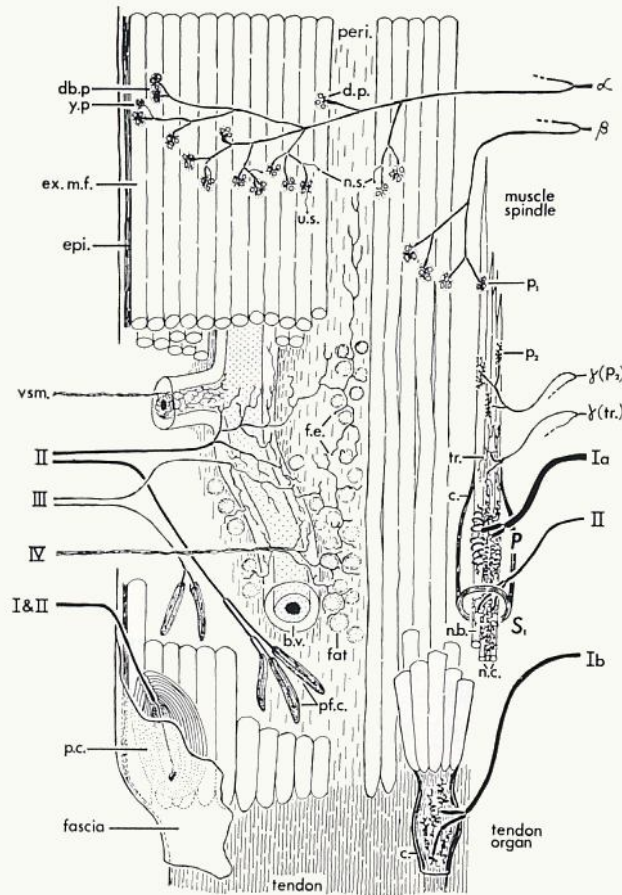


FIG. 20. Schema of the innervation of mammalian skeletal muscle based on a study of the cat. Those nerve fibres on the right of the diagram are exclusively concerned with muscle innervation; those on the left also take part in the innervation of other tissues. Roman numerals refer to the groups of myelinated (I, II, III) and unmyelinated (IV) sensory fibres; Greek letters refer to motor fibres. Features of terminal sprouting and degeneration are omitted from the spindle. b.v. = blood vessel; c = capsule; db.p. = double motor end-plate; d.p. = degenerating end-plate; epi. = epimysium; ex.m.f. = extrafusal muscle fibre; n.b. = nuclear-bag intrafusal muscle fibre; n.c. = nuclear-chain intrafusal muscle fibre; n.s. = nodal sprout; P = primary ending; p₁, p₂ = two types of intrafusal end-plates; peri. = perimysium; p.c. = Pacinian corpuscle; pf.c. = paciniform corpuscle; S₁ = secondary ending; tr. = trail ending; u.s. = ultraterminal sprout; vsm. = vasomotor fibres; y.p. = young motor end-plate ("accessory ending"). (Barker, *Myotatic, kinesthetic and vestibular mechanisms*, Ciba Found. Symp., London, 1967).

36% in cat hindlimb muscles (Barker, 1959); *complex* ones with P plus a variable and larger number of S, occurs in many spindles from limb muscles. Measurements of the relative number of P and S endings have been published by several authors (Swett & Eldred, 1960b; Barker, 1962; Boyd, 1962; Eldred, Bridgman, Swett & Eldred, 1962 and below).

The discovery of the nuclear chain intrafusal fibres by Cooper & Daniel (1956, man) and Boyd (1956, cat) did not annul this principle of classification but refocused attention on the problems of site and mode of innervation of primaries and secondaries. The schematic Fig. 21 should be of some help in following the description of afferent

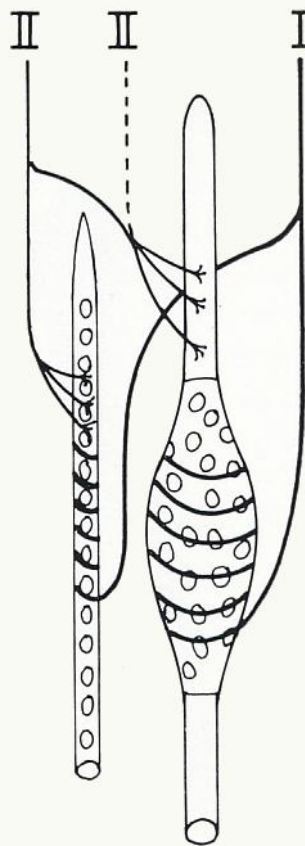


FIG. 21. Diagram of afferent innervation of nuclear bag (right) and nuclear chain fibre (left). It is uncertain whether all secondary endings on myotube region of nuclear bag are innervated by branches of afferents from the nuclear chain fibre.

spindle innervation. The various types of sensory endings to be described will be found illustrated in Fig. 22. The general description is given for the cat according to Boyd (1962) but both Barker and co-workers and Cooper & Daniel are in essential agreement with its main features.

The spirals and rings which together make up the primary ending in any one encapsulated unit are found equatorially located on both bag

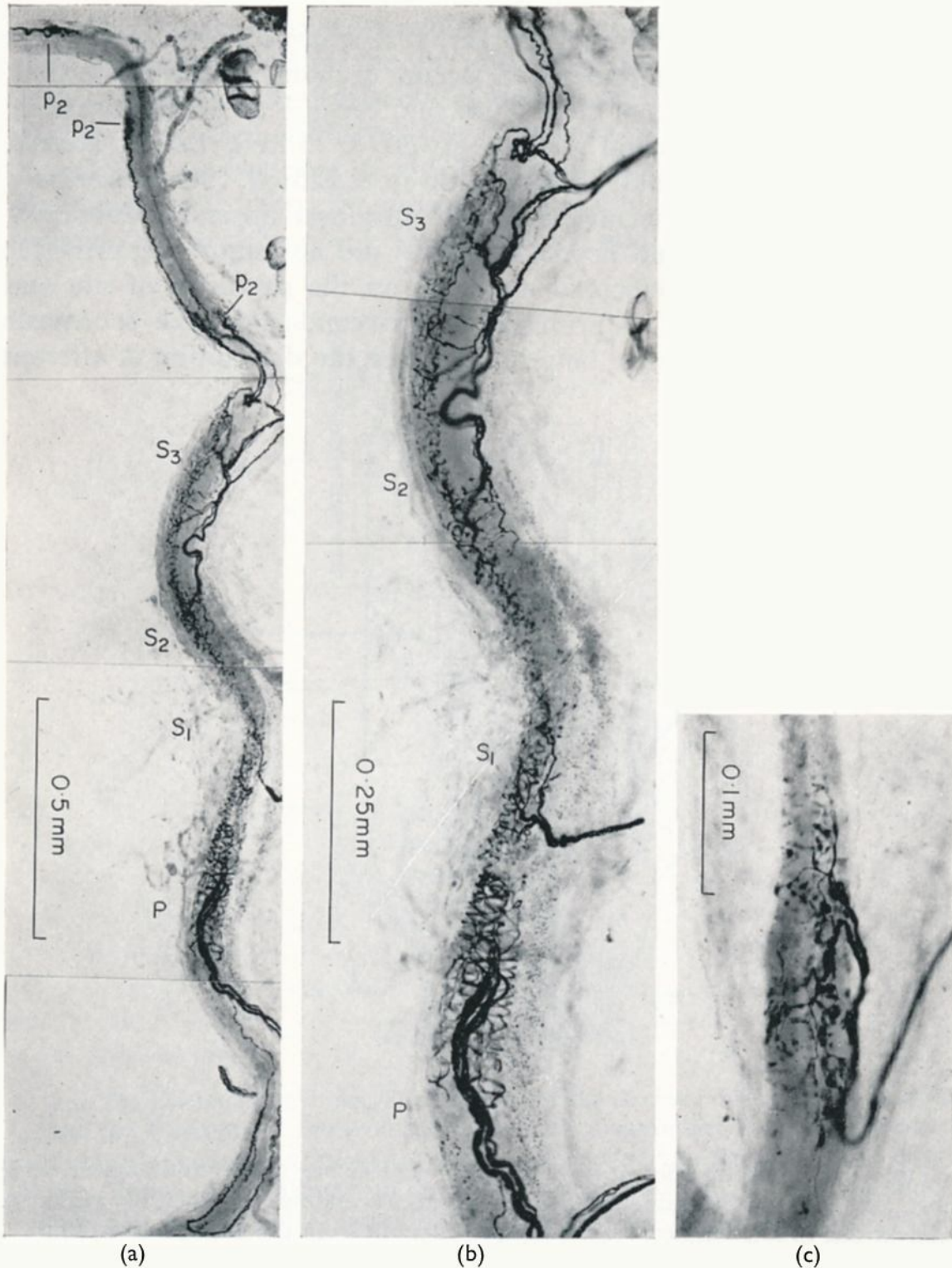


FIG. 22. Cat. (a) Muscle spindle with primary and three secondary endings from normal tenuissimus. Note clarity of motor innervation in this silver preparation. (b) Enlargement of the sensory innervation of the spindle shown in (a). The secondary endings are located mainly on the nuclear-chain muscle fibres (coursing through on the left-hand side of the spindle) and only to a small extent on the nuclear-bag muscle fibres. (c) Secondary ending of the flower-spray type in de-efferented peroneal spindle. Marked as Fig. 20. (Barker, *Myotatic, kinesthetic and vestibular mechanisms*. Ciba Found. Symp. London, 1967).

and chain fibres (these are of smaller diameter in the chain fibres, which are themselves smaller) and each spiral receives a branch from the large afferent fibre belonging to the functional Group I in Lloyd's (1943a) well-known classification. These are nowadays (Bradley & Eccles, 1953) called Ia to distinguish them from Ib fibres supplying the Golgi tendon organs. The afferents of secondaries belong to Group II. The Ia fibre does not branch to other spindles and therefore transmits a message conditioned by the properties of all the primary coils of one particular bag-chain intrafusal combination. This description is valid also for the simple spindles (type P) whose "simplicity" exists merely in the absence of a message from secondaries. The motor innervation of their two types of intrafusal fibres are as in complex spindles. The large majority of the secondaries (in spindles with both types of intrafusal fibres) are found on the chain fibres, with a minority on the bag fibres. Cat spindles may be provided with up to five (Boyd) or four (Barker & Ip, 1961) secondaries each of them extending over a region 300–550 μ in length. Boyd speaks of a P region, occupied by the primary ending, and of a number of S regions, each about 300 μ , to either side of it. The secondaries are found in the regions S_1 to S_3 , the majority in S_1 and S_2 but some definitely outside the region of chain nuclei as far away from the primaries as to be in S_3 . The distance from S_1 to S_3 implies an increasing amount of striation so that the S_3 secondaries far away from the equator actually innervate the polar region. Some secondaries are likely to lie close to motor endings, as emphasized by Coërs (1967). They are all supplied by branches of Group II fibres. The latter may sometimes also be distributed to secondaries in other spindles (confirmed by Wohlfart & Henriksson, 1960, in mouse spindles). In the muscles used by Boyd, soleus, tenuissimus and an interosseus, there were 1.5 secondaries to every primary. Since most cat muscles possess secondaries, their spindles belong to Ruffini's *complex* group, Barker (1959) refers to the spindles with one primary and one secondary ending (P + S) as *intermediates* which was the original term used by Ruffini in his classification.

Boyd considered the possibility that Ruffini's flower-spray endings, which in his own slides appear as black dots, may be part of a small spiral in which the very thin connecting links between the dots have remained unstained. He finds flower-sprays more commonly represented among the secondaries. Barker & Ip (1963) have recently improved the de Castro method of silver impregnation and their observations on secondaries have been summarized by Barker (1967) as follows: "Those secondaries that lie nearest to the primary endings consist chiefly of rings and spirals and are supplied by thicker axons than those located

further away, which have a more irregular 'flower-spray' form. Annulo-spiral secondaries are about twice as common as flower-spray secondaries in the cat. In spindles with a secondary innervation, the primary ending is generally supplied by a larger diameter Ia fibre than those without." If there are two types of secondaries this, together with their variable location, is something for physiologists to consider from the functional standpoint. The afferents from spindle secondaries belong to Group II in Lloyd's classification.

Table 3 (Barker, 1962) shows the distribution of primaries, secondaries, Golgi tendon organ and paciniform corpuscles in a number of cat muscles. In tandem spindles each encapsulated unit has been counted as a separate sense organ.

TABLE 3

Proportional Distribution of Afferent Endings in Various Cat Muscles^a

Muscle	No. studied	Total no. endings				Ratios			
		P	S	TO	PC	P:S		P:TO	
						range	av.	range	av.
Rect. fem.	9	920	899	705	114	0.9-1.5:1	1.0:1	0.7-2.4:1	1.3:1
Soleus	3	164	130	92	6	1.0-1.4:1	1.3:1	1.7-1.9:1	1.8:1
ST	3	411	489	257	10	0.7-1.0:1	0.85:1	1.2-1.85:1	1.6:1
Mesial FDL	1	51	47	17	2	—	1.1:1	—	3.0:1
V pes int.	4	108	64	99	34	1.3-2.3:1	1.7:1	0.9-1.6:1	1.1:1
IV intercostal (int. and ext.)	1	49	67	17	10	—	0.7:1	—	2.9:1

^a From Barker, *Symposium on muscle receptors*. Hong Kong, 1962.

Abbreviations used: P = primary; S = secondary; TO = tendon organ; PC = paciniform corpuscle.

Tandem Spindles

Among those who have described tandem spindles in mammals there is fair agreement about the way they are designed (Cooper & Daniel, 1956, 1963; Barker, Cope & Ip, 1960; Swett & Eldred, 1960a; Barker, 1962; Boyd, 1962; Voss, 1962). Only one or two fibres of the nuclear bag type run through the tandem equipage and if this is not the case, the spindles may be said to be end-to-end but not true tandems. The short chain intrafusal fibres are restricted to each individual capsular unit of the series. The nerve supply is independent for each of them but Cooper & Daniel report that the large through-fibre of bag type may be innervated from one spindle only so that the contraction is trans-

mitted from it to the next one of the tandem. Usually the first capsule of the series is complex and the rest may be simple (Boyd, 1962). Barker, summarizing the work with Cope & Ip, states that in the cat the first capsule of a tandem is larger, with ten to twelve muscle fibres which contain one primary and two or three secondary endings, and is followed by one or more capsules bearing a primary ending only. The most common tandem is a doublet. Swett & Eldred found 31–44% tandem spindles in the medial gastrocnemius muscle and 11–21% in the soleus of the cat. Among the tandem spindles in its rectus femoris Barker *et al.* (1960) found 88% double, 9% triple and 3% quintuple.

Clearly the tandem spindles in the limb muscles are common enough to be functionally significant though Voss (1962) found only 6% in the lumbricals. Swett & Eldred noted that in short muscles of the cat a tandem spindle might run from the proximal to the distal tendon and concluded that they serve to measure the average length of a muscle or of a large portion of it.

Problems of Distribution

Considering the large range of contraction times of extrafusal fibres of twitch muscles some authors (Swett & Eldred, 1960b; Homma & Seki, 1964) have looked for systematic differences in the organization of the spindle receptors in slow and fast muscles. So far the results have not been very rewarding and it seems likely that systematic differences, inasmuch as they occur at all, would be best developed on the motor side of spindle innervation. This is as yet, however, an unwritten chapter. Homma & Seki found in the soleus, gastrocnemius and tibialis anterior of cat and monkey—which represent a series of decreasing contraction times—that the diameter of the largest ring around the nuclear bag increased in the same order. Swett & Eldred, comparing gastrocnemius and soleus in the cat, saw more short intrafusal fibres in the gastrocnemius and found the spindles in the soleus to be larger in all dimensions. In view of the differentiation of contraction times within the motor units of one muscle (Chap. I) it is difficult to evaluate such findings without knowing whether the spindle was located in a relatively slow or fast motor unit. Gastrocnemius, for instance, contains a large number of motor units as slow as those in soleus. It may, however, be functionally relevant that in gastrocnemius the spindles extended over one-third of the fascicle length, in soleus over only about one-fifth (Swett & Eldred).

There are counts of number and descriptions of distribution of muscle spindles in the hindlimb muscles of the cat by several authors (Hagbarth & Wohlfart, 1952; Barker & Chin, 1960; Swett & Eldred, 1960a;

Boyd, 1962; Chin, Cope & Pang, 1962; Eldred *et al.*, 1962). The difficulties experimenters encounter may be illustrated by the soleus of the cat in which on an average (Table 3) there are 55 primaries, 43 secondaries and 31 tendon organs. As we shall see, the two latter endings are inhibitory, the primaries excitatory on motoneurons of ankle extensors and so what matters is the unknown algebraical sum of two minus and one plus term; all terms, and in particular the minus terms, are also dependent on the state of the interneurons on the route. This means that only general features such as density (number of capsules per g), location along the nerve stems and preferentially in the fleshy portion of a muscle as well as the correlation with afferent fibre size (conduction velocity) have been made use of in considering spindle function. Some characteristic pictures of the distribution of spindles in cat hindlimb muscles are shown in Fig. 23 from the papers of Hagbarth

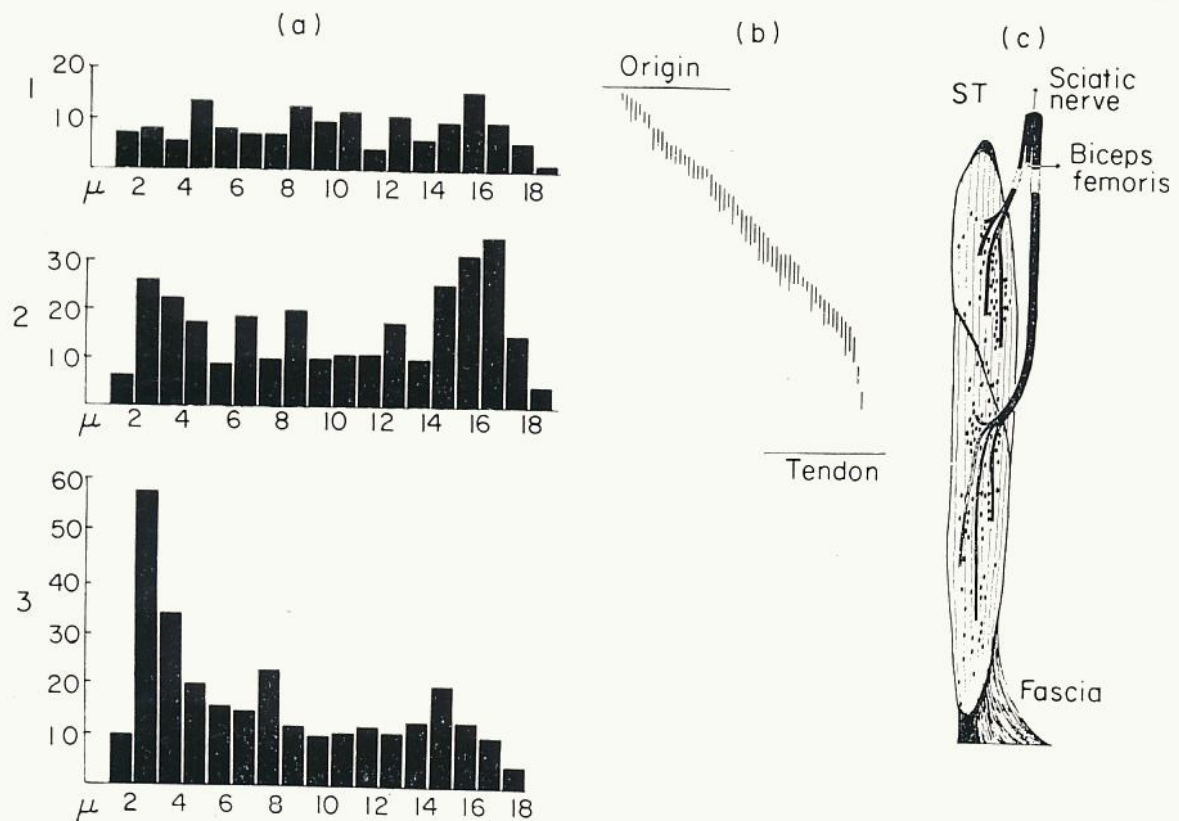


FIG. 23. (a) Number of muscle afferent fibres of different size plotted against fibre diameter in μ (calibre spectrum). 1: soleus, 2: gastrocnemius medialis, 3: tibialis anterior. (b) Distribution of muscle spindles in soleus. (Hagbarth & Wohlfart, *Acta anat.*, 1952. Figs 8, 11, 12, 13. Karger, Basel, München, New York, 1952.) (c) Projection plans of cat semitendinosus muscle showing distribution of spindle capsules (black oval symbols) and nerve supply. Nerve branches shown black up to point of entry into muscle. (Chin, Cope & Pang, *Symposium on muscle receptors*, Hong Kong, 1962).

& Wohlfart (1952) and of Chin *et al.* (1962). Table 4 serves to illustrate spindle densities in some muscles from the same animal, so much used in experimental studies of spindle function.

TABLE 4
Number and Density of Spindle Capsules^a

Muscle	Mean weight (g)	Spindle capsule-content Range	Mean and s.d.	No. spindle capsules/g
Lat. gastroc.	7.61	21 (25 to 45)	35 ± 7	5
Mes. gastroc.	7.34	35 (46 to 80)	62 ± 9	9
Rect. fem. ^b	8.36	56 (77 to 132)	104 ± 14	12
Tib. ant. ^b	4.57	38 (52 to 89)	71 ± 9	15
ST	6.41	62 (80 to 141)	114 ± 14	18
Soleus	2.49	31 (40 to 70)	56 ± 7	23
FDL lat.	3.25	34 (58 to 91)	75 ± 8	23
Tib. post.	0.78	19 (21 to 39)	31 ± 4	39
FDL mes.	1.06	24 (36 to 59)	48 ± 6	45
Vth int. (foot) ^c	0.33	12 (22 to 33)	29	88
Vth int. (hand) ^b	0.21	11 (21 to 31)	25 ± 2	119

^a Chin, Cope & Pang (1962). *Symposium on muscle receptors*, Hong Kong.

^b Data from Barker & Chin (1960).

^c Four muscles counted (Ip, 1961).

Number and Density of Spindle Capsules

It is seen that, for instance, gastrocnemius has few spindles by comparison with soleus, as first pointed out by Hagbarth & Wohlfart (1952). Similarly it emerges that the small muscles at the end of extremities have high spindle densities as also found by Cooper (1960), Cooper & Daniel (1963) and particularly by Voss (1937) and by Schulze (1955) who have published extensive measurements of the relative number of muscle spindles in man (see below). "The muscle spindles of different mammals have many points in common and there is nothing in the present work to suggest that human spindles have a specific pattern beyond the fact that they are longer and often have more intrafusal muscle fibres, including the bigger nuclear bag fibres, than the better known spindles of the cat and rabbit" (Cooper & Daniel). A large number of species have been used in the study of muscle spindles. These have not been mentioned here but have been listed by Huber & De Witt (1897), Baum (1900), Hinsey (1934), Cooper (1960), Keene (1961), Estable & Cenoz (1962) and in the

valuable bibliography of literature on muscle receptors by Eldred *et al.* (1967).

Spindles in organs like the extraocular eye muscles, the diaphragm and the respiratory muscles will be mentioned in connection with experimental work on these structures.

The extensive spindle counts in man carried out by Voss (1937, 1956a, b, 1958, 1959) on newborn infants indicate patterns of distribution which must have functional significance. The index of comparison used by Voss, number of spindles per 1000 mg, is based on standard weight tables (Voss, 1956a) for the various muscles studied and thus cannot be free from errors, but the major variations are of an order of magnitude beyond criticism. Some examples: *m. serratus post. inf.* (18.8 g) contains 56 spindles (index = 2.94) while *m. longissimus capit.* (8.0 g), which hardly weighs half as much has 507 spindles (index = 63.3). Cooper (1966b) also states that in her experience the muscles richest in spindles are the deep ones connecting the vertebral column with the head which have "a bewildering number of spindles". Some of Voss' other index figures are: hip and upper part of leg, below 5.0; shoulder muscles as low as 0.6; forearm *brachioradialis* 1.03; again, pronators and supinators spindle-rich with indexes from 5.0 to 10.0. To the latter category also belong the lumbricals. For a table of values see Voss (1963).

The figures suggest that muscles undergoing small length variations requiring precision also require elaborate spindle control. The muscles controlling position of the head and pronation-supination belong to that category. An important postural task for a muscle is thus likely to be reflected in a large index figure.

Further references to papers containing some spindle counts will be found in Cooper's (1966a) analysis of the relation between number of muscle spindles and number of myelinated nerve fibres to a muscle, as given in Fig. 24. The fibre counts in man are based on the data of Feinstein, Lindegård, Nyman & Wohlfart (1955) and Christensen (1959), those for the cat and the rat on the papers of Boyd & Davey (1962, republished and completed 1968) and Mellström & Skoglund (1965) respectively. Using these data Cooper has drawn a line indicating the position for which the number of spindles would be 10% of the number of nerve fibres. For some muscles there are two figures to indicate different estimates. Spindle-rich muscles would be to the right of the line. There are a number of unexplicable values in the diagram (for example *tibialis ant.* or T.A. and *masseter*) suggesting errors, discussed by Cooper, but as a first attempt at a synthesis of available data it is nevertheless of considerable interest.

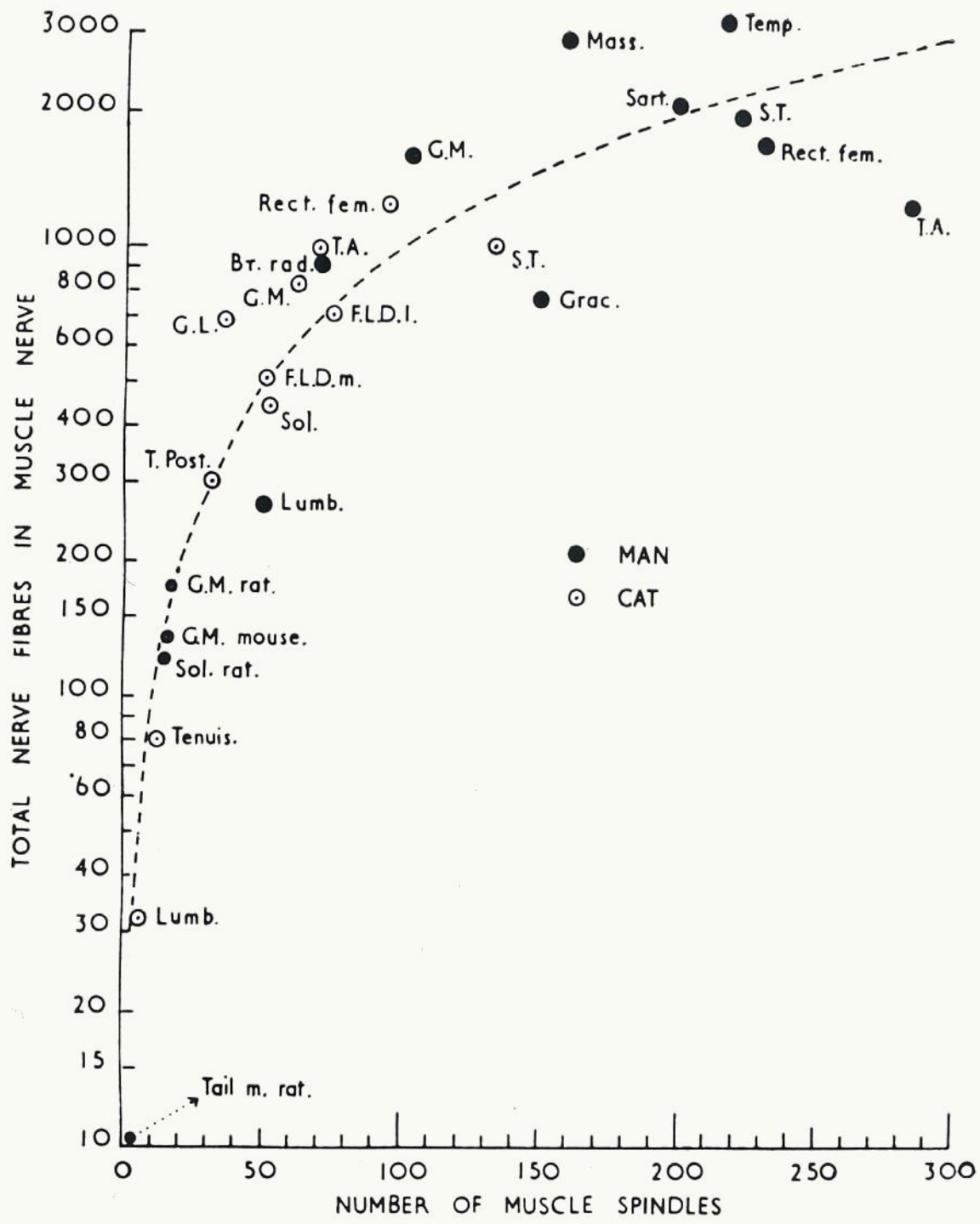


Fig. 24. Total number of myelinated nerve fibres to a muscle plotted against the total number of muscle spindles in the muscle. Values from man, cat, rat and mouse are given. The dotted line indicates the position where the number of spindles would be 10% of the number of nerves. Numerous points lie on this line. Some scatter of the values for spindle-poor muscles to the left and of spindle-rich muscles to the right may be normal, but a big deviation from the line suggests erroneous counts. (Cooper, *Control and innervation of skeletal muscle*, Dundee Symp., 1966a).

THE TENDON ORGANS

Huber & De Witt (1900), who have given a good historical account of the work in this field, distinguish a pre-Golgi era from the epoch following after Golgi's (1903a) description (1870–83) of the dominant sense organ in the tendons which afterwards was to be called the Golgi tendon organ. Golgi himself named it the "organo nervoso musculo tendineo". The term emphasized that it was found located in the tendon at the border between muscular and tendinous tissue. Wohlfart & Henriksson (1960) studying the mouse gastrocnemius, underline that this holds good for both the origin and the insertion of the muscle so that it is impossible to paralyse selectively the tendon organs by cocainizing the muscle's distal end alone. Golgi's work was confirmed and extended by several histologists among whom might be mentioned Cattaneo (1888), Ciaccio (1890), Mazzoni (1890), Ruffini (1897–98) and Huber & De Witt (1900). The recent development has been fully reviewed by Poláček (1966) who also reports work of his own and includes plates illustrating all of the types of end organ found in the joints. Since 1900 nothing fundamentally new has been added by techniques based on the light microscope Merrillees (1962) has pioneered an electron microscopic study of the Golgi tendon organs in the rat

Stilwell (1957a, b, c, d) speaks of tendon organs as a "Ruffini triad". This terminology does not add much to the clarity arrived at by the early workers, all of whom have called attention to corpuscles of small size, independent, or, alternatively, situated in close contact with the large musculo-tendinous organ of Golgi. The Italian anatomists from Golgi onwards, for example Ruffini (1890) describe these structures as paciniform endings or Golgi–Mazzoni corpuscles and point out that some of them have the inside club-like structure of the typical Pacini body, others possessing a complex network not very different from the sprays of terminals characterizing the true Golgi organ. The latter is illustrated (Fig. 25) by drawings of Ciaccio, elegant specimens of the technique of that period. The drawings demonstrate their size which in man may amount to 2–3 mm in length and 1.1–1.5 mm in width. In the cat they average 0.5 by 0.1 mm and each Golgi tendon organ is connected in series with about ten extrafusal fibres (Barker, 1967, as based on extensive work within his Hong Kong group). These belong to different motor units.

The tendon organs have been seen and studied throughout the vertebrate phylum. From birds upwards they become encapsulated and in the higher species they increase in complexity as a consequence of the increasing number of medullated branches that go to form a likewise

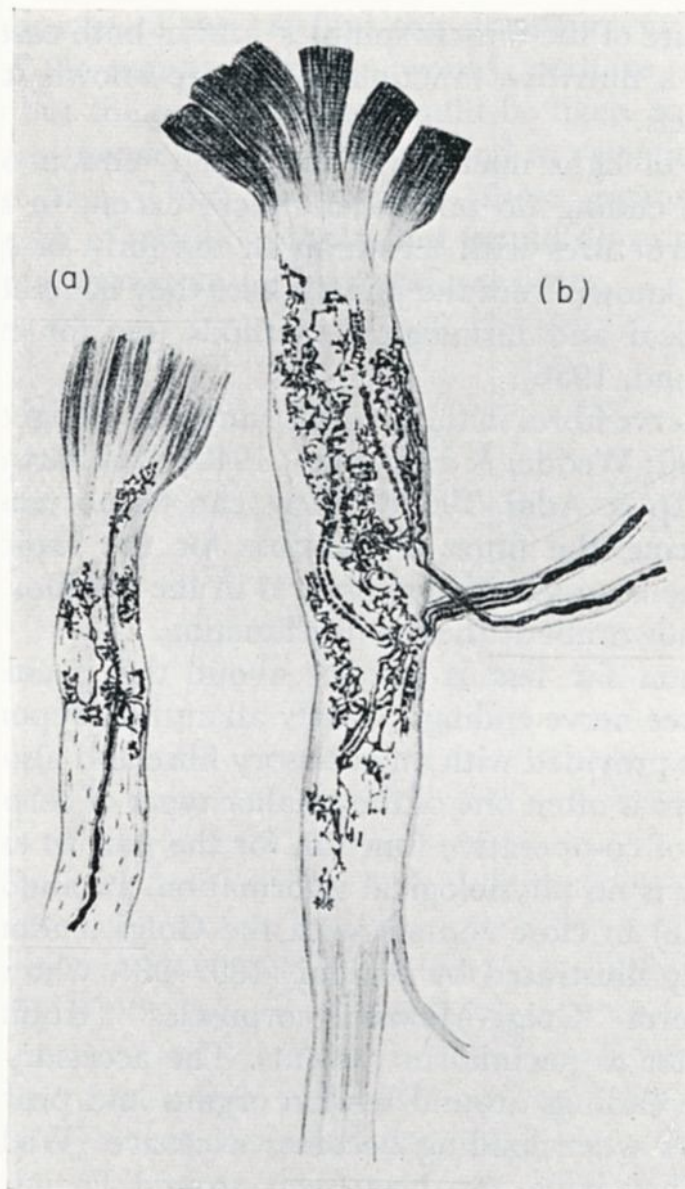


FIG. 25. Two Golgi tendon organs from the Achilles tendon of rat (left, $\times 98$) and man (right, $\times 147$). (Ciaccio, *Mem. Reale Acad. Sci.*, Bologna, 1890).

increasing number of the non-medullated sprays of terminals which are described as clasping one or several of the small bundles of connective tissue making up the tendon fibrils. According to Merrillees (1962) the latter are occasionally in direct contact with the plasma membrane of the nerve endings but more often they are separated by basement-membrane material or by very thin processes of Schwann cells. The whole organ is often spindle-shaped and, apparently for this reason, is sometimes called a tendon spindle; at times its shape is cylindrical, regularly so, for instance in the eye muscles (Huber, 1900). In the electron microscope the structure of its capsule cannot be distinguished

from the structure of the muscle spindles' and in both cases the capsules probably have a nutritive function. They are known to be provided with blood vessels.

At the level of light microscopy the Golgi tendon organ and the smaller Ruffini ending do not differ much, except in size; both are encapsulated structures with terminals in the form of sprays. Ruffini organs are well known from the joints where they have been studied by both physiological and histological methods (see for example Boyd, 1954; S. Skoglund, 1956).

The largest nerve fibres in the tendons run to the Golgi organs (Huber & De Witt, 1900; Weddell & Harpman, 1940; Wohlfart & Henriksson, 1960; Barker, Ip & Adal, 1962). There can be no reasonable doubt about those being the fibres responsible for the rapidly conducted impulses from tension-sensitive structures in the tendons (Chap. V). A great deal is known about their reflex function.

By comparison far less is known about the paciniform, Golgi-Mazzoni and free nerve endings. Nearly all authors report that a Golgi tendon organ is provided with an accessory fibre and also that, clinging to its body, there is often one of the smaller types of corpuscle, suggesting some kind of co-operative function for the pair to execute, but on this point there is no physiological information. Paciniform corpuscles (club-like inside) in close contact with the Golgi tendon organs have been beautifully illustrated by Ruffini (1897-98), who also is responsible for the term "Golgi-Mazzoni corpuscles" (Ruffini, 1890) and regards the latter as paciniform variants. The accessory fibres form a network of free endings around tendon organs and probably transmit "pain" impulses when loading becomes excessive (Weddell & Harpman, 1940). They have also been seen around Pacini bodies in the deep fascias of elbow and ankle joints in man. On the functional side physiologists have been restricted to identification of small corpuscles in terms of Lloyd's fibre Groups II and III of afferent conduction velocities without specification of the particular type of end organ from which these fibres arrive (Chap. V). The tendons are generally held to be innervated exclusively by muscle nerves (Hines, 1927; Hinsey, 1927-28; Hines & Tower, 1928; Tiegs, 1953) but in man exceptions from this rule have been noted by Wrethe (1956).

In Table 3 (p. 50) will be found figures for the distribution of Golgi tendon organs and paciniform corpuscles in a number of cat muscles.

Sherrington (1894) described spindles in series with tendon organs and his observations were confirmed by Barker (1948). Recently Eldred and his co-workers (Bridgman, Shumpert & Eldred, 1969; Eldred, personal communication) have re-investigated this question

and in some muscles of the cat find this arrangement quite common. The spindle of the combined organ would, perhaps, not differ from other spindles but the tendon organ would be likely to measure intrafusal tension and hence, reflect and respond to variations in intrafusal properties and bias. Thus, for instance, these organs would hardly respond to stretch of passive spindles but would do so under fusimotor alpha or gamma activation of the intrafusal fibres.