Distribution, density and size of muscle receptors in cat tail dorsolateral muscles

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INTRODUCTION

In cat tail, a thin sheet of dorsolateral muscle is found bilaterally. When the muscle is exposed by lateral retraction of longitudinally running dorsolateral tendons, individual muscle spindles and Golgi tendon organs can be seen under a dissecting microscope. This easy accessibility has prompted considerable experimental work on these muscle receptors.

Hunt, Adal, Beacham & Heistracher (1972) provided the initial study of the muscle spindles, whose morphological and physiological characteristics were found to be generally similar to those previously described for mammalian hindlimb muscle spindles. In muscle spindles *in vitro*, isolated from the cat tail muscle, the discharge patterns and receptor potential in response to ramp-and-hold as well as to sinusoidal stretches have been analysed (Hunt & Ottoson, 1975, 1976, 1977; Hunt & Wilkinson, 1980). The ionic mechanism underlying the receptor potential has also been studied (Hunt, Wilkinson & Fukami, 1978).

Tail muscle Golgi tendon organs have also been isolated and studied *in vitro* with intact sensory innervation. Fukami & Wilkinson (1977) described the impulse and generator potential responses to ramp-and-hold mechanical stimulation of single Golgi tendon organs. Fukami (1980) analysed the interaction of impulse activity elicited by mechanical stimulation of two Golgi tendon organs innervated by the same afferent axon.

The purpose of the present work is to provide information on the segmental distribution of these receptors in the cat dorsolateral tail muscles. By noting the location in the muscle and the size of each capsule, maps of the entire complement of receptors were constructed. Information was derived about receptor size and location. The bilateral symmetry of receptor incidence, as well as the Ia/Ib afferent fibre ratio, suggested fine control of the contraction of these muscles by the central nervous system. A preliminary report of the data has been given elsewhere (Goldfinger & Fukami, 1980).

MATERIAL AND METHODS

Three adult male cats (2–4 kg) were anaesthetized with sodium pentobarbital (40 mg/kg, I.P.). The tail was skinned and removed at the segment where the base first protrudes from the body wall (corresponding to the fifth caudal segment in two

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cats and the fourth segment in another) and placed in a Locke solution bath. Using magnet-based tungsten wire hooks, the entire dorsolateral muscle on both sides was exposed to the bathing solution by lateral retraction of the dorsolateral tendons.

For staining, the entire tail was subsequently exposed to a solution of 1 or 2·5 % OsO_4 in 0·1 M cacodylate buffer for 20 to 40 minutes, washed in Locke solution, divided into respective caudal segments, and stored in glycerol (Adal & Barker, 1965; Gladden, 1969). Subsequent additional staining, which was often needed for segments with a large mass of muscle, could be done by further exposure to the OsO_4 solution, even weeks after the initial staining.

For examination, the segmental muscle bundle on each side was detached from the periosteum at its origin, and connective tissue was removed as much as possible. The larger muscle bundles were subdivided into thirds (rostral, middle and caudal), which were further subdivided if necessary.

Under a dissecting microscope, darkly stained myelinated nerve fibres were readily recognizable within the mass of muscle. Nerves could be traced to their terminal branches on extrafusal muscle fibres and in muscle spindles, or in Golgi tendon organs. The adequacy of the nerve staining was evidenced by the identifiable innervation of individual extrafusal muscle fibres examined.

For each isolated receptor, measurements were made to the nearest 10 μm of the capsular length, the maximum equatorial width of the capsule, and, for spindle capsules, the distance from the equator to the tendon. This measurement of capsular length corresponds to that of Barker & Ip (1961) who defined the 'capsule length' of muscle spindles as the length of fusiform swelling. For Golgi tendon organs, this measurement is less precise, due to the gradual tapering of most of their capsules. Neither the capsule position, with respect to the muscle bundle thickness, nor the total length of muscle spindles were measured.

For the capsules of Golgi tendon organs, in addition to the above measurements, the number of muscle fibres inserting directly into the receptor was counted. The branching of one myelinated axon to innervate more than one Golgi tendon organ capsule (Fukami, 1980) was also noted.

The accurate localization of a capsule equator with respect to the rostrocaudal axis of a given segment was compromised by the intermingling of muscle fibres of adjacent muscle bundles, as well as by the disruption of the muscle bundle organization required for isolation by dissection. Thus the resolution of such localization was limited to a third of a segment length.

After examination, segmental muscle bundles for each side were washed in Locke solution, blotted on tissue paper to remove excess fluid, and weighed. In a separate tail, there was a correlation ($r = 0·932$, $N = 8$) between the wet weight of a muscle bundle and the number of muscle fibres counted therein using conventional histological technique (20 μm thick sections stained with toluidine blue). Assuming uniform muscle lengths, the proportionality constant was 18 muscle fibres per mg wet weight.

For correlation analysis of scatter plot data, estimators used to determine the significance of correlations are given in Table 1. A correlation between two parameters was considered to be established when the (product-moment) correlation coefficient exceeded the upper limit for non-correlation at the 95 % significant level (Dunn, 1964; Goldstein, 1964; see Diem & Lentner, 1970).

Table 1. *Scatter plot correlation analysis*

	Regression line		Correlation coefficient				
	Slope	Confidence range	r_{min}	r^*	Confidence limits on r	N	Correlated?
Spindles Length, width	0·114	0·100–0·127	0·101	0·652	0·590–0·707	373	Yes
Golgi Tendon organs Length, width	0·057	0·044–0·069	0·110	0·450	0·357–0·534	315	Yes
Golgi tendon organs Width, no. input muscle fibres	0·066	0·049–0·083	0·111	0·394	0·295–0·484	308	Yes
Spindles Length, location on muscle	0·011	0·001–0·022	0·101	0·108	0·007–0·207	373	No
Spindles Width, location on muscle	0·096	0·036–0·157	0·101	0·161	0·061–0·258	373	Yes
No. spindles vs. no. Golgi tendon organ (segmental)	0·760	0·663–0·857	0·259	0·903	0·840–0·941	58	Yes
No. spindles vs. no. Golgi tendon organ ($\frac{1}{3}$ segmental)	0·601	0·454–0·747	0·199	0·639	0·504–0·743	98	Yes
Muscle mass *L* vs. *R* (segmental)	0·918	1·07–0·768	0·396	0·935	0·856–0·971	25	Yes
No. spindles *L* vs. *R* (segmental)	0·839	0·691–0·987	0·396	0·926	0·837–0·968	25	Yes
No. Golgi tendon organ *L* vs. *R* (segmental)	0·834	0·599–1·069	0·396	0·837	0·660–0·926	25	Yes

* r is the correlation coefficient. If r exceeds r_{min}, the hypothesis of *no* correlation is rejected (Diem & Lentner, 1970).

RESULTS

Segmental contents over the length of the tail

The entire sample of receptors in those muscles located in caudal segments 5–15 (cats 1 and 3) or 4–13 (cat 2) consisted of 373 muscle spindle capsules and 315 Golgi tendon organ capsules. For each tail, the most rostral segment studied was the first to protrude from the body wall; beyond the most caudal segment studied, no segmental dorsolateral muscle was found. The dorsolateral muscle was also absent in right side 14th and 15th segments of cat 1, right side 11th, 14th and 15th segments and left side 13th to 14th segments of cat 2, and left side 14th and 15th segments of cat 3.

For each whole tail side, the muscle mass and number of receptor capsules decreased gradually from the base towards the tip. An example of the location of muscle spindles and Golgi tendon organs along the length of the tail of cat 1 up to the 12th segment is given in Figure 1.

Irrespective of the segmental position in the tail, there was a correlation between the numbers of spindle and Golgi tendon organ capsules (Table 1). Typically the number of spindle capsules exceeded the number of Golgi tendon organ capsules. From the regression on the scatter plot, the relationship between the number of spindle capsules (n_S) and the number of Golgi tendon organ capsules (n_G) was:
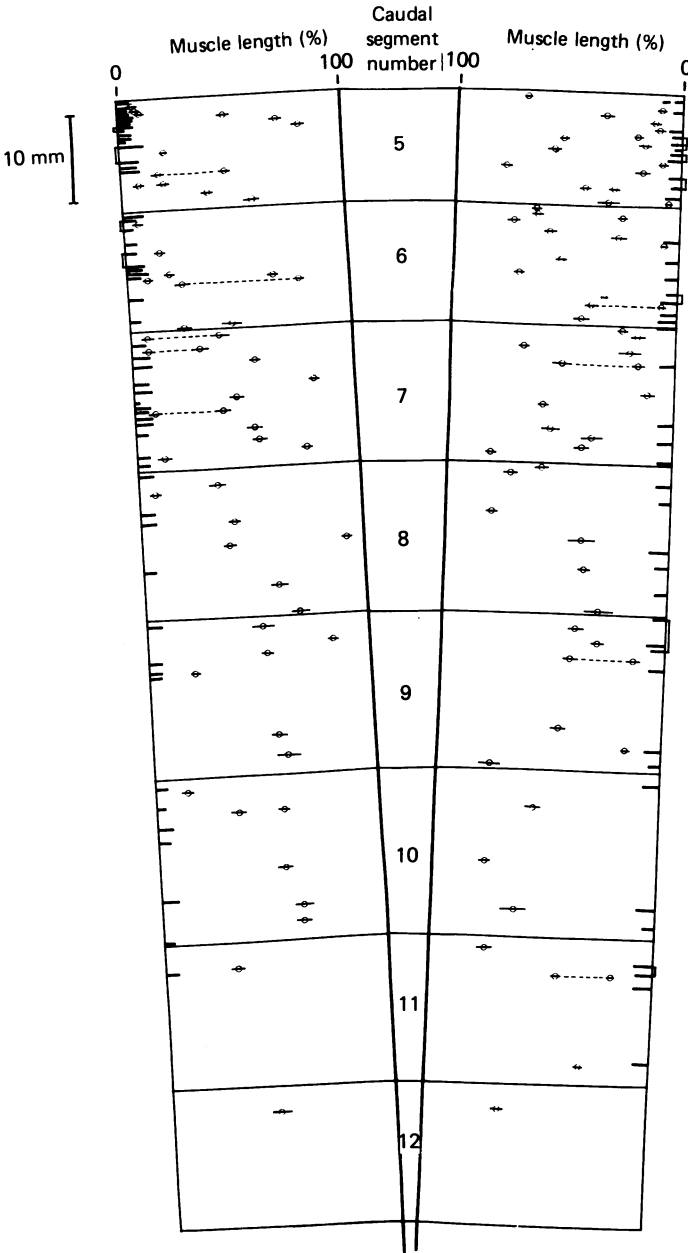
$$n_G = 0·76 n_S + 0·55.$$

Fig. 1. Map of locations of muscle spindles and Golgi tendon organs in dorsolateral muscles of cat tail, shown as a dorsal view. The muscles are exposed on both sides of the segmental tail bones by lateral retraction of the tendons. Mechanoreceptor capsules are indicated by respective symbols: circles with bisecting line for muscle spindle; bar for Golgi tendon organ. Abscissa: Relative extrafusal muscle length expressed as extending from the tendon (0 %) to the periosteum (100 %) from which the muscle originates. Actual extrafusal muscle lengths ranged from 15–18 mm. Capsular lengths are drawn relative to the segmental extrafusal muscle length and indicated by the length of each symbol line (spindles) or bar (Golgi tendon organs). Tandem spindle capsules are shown connected by a dashed line. Ordinates: Actual rostrocaudal segmental length drawn to scale. In this cat, caudal segment no. 5 was the first to protrude from the body wall. Capsule widths are not indicated by the standard symbols (see Fig. 5 for capsular width data). Golgi tendon organs innervated by the same axon are connected by a line at their respective tendon base. Errors for the actual capsular position on this axis are within one third of a segmental length.
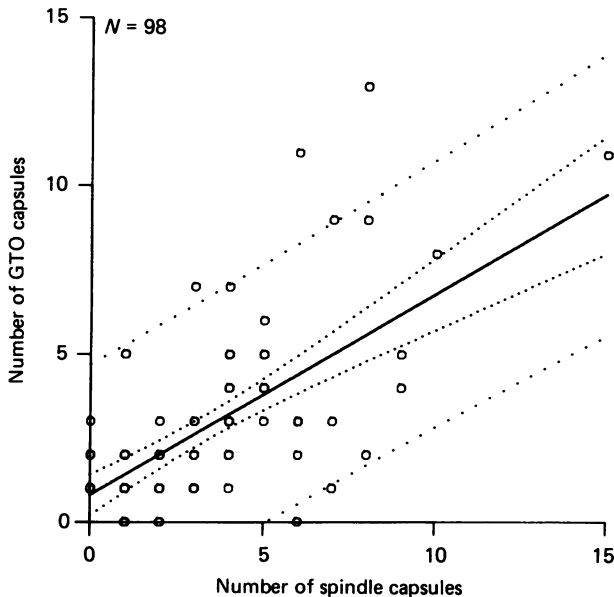
Fig. 2. Scatter plot of number of spindles *vs.* number of Golgi tendon organs. Each datum point was obtained for the muscle mass of one third of the rostrocaudal length of a given segment. This and all subsequent scatter plots also show (i) computed regression line as a solid straight line, (ii) 95 % confidence limits on the mean *Y* predicted for any *X*, as curvilinear dotted lines closest to the regression line, and (iii) 95 % confidence limits on *Y* predicted for any *X*, as curvilinear dotted lines farthest from the regression line. That is, based on the computed correlation (Table 1), for any value of *X*, *individual* values of *Y* will fall within the *outer* dotted boundary, and *average* values of *Y* will fall between the *inner* dotted boundary. Note that several plotted datum points are superimposed.

A similar relation obtained for data from thirds of a segment (Fig. 2; Table 1):

$$n_G = 0.60n_S + 0.82.$$

Slightly greater numbers of spindles than Golgi tendon organs have been reported for various cat muscles whose total mass approximates or exceeds that of the tail muscle (see Table 1.2, Matthews, 1972).

Ipsilateral contents and bilateral symmetries

The average total numbers of receptor capsules per whole tail side were: 63 spindles (range: 56–71) and 53 Golgi tendon organs (range: 43–58). The average total ipsilateral muscle wet weight was 472 mg (range: 306–670 mg). Thus, the average ipsilateral receptor densities were: 142 spindle capsules per gram (range: 92–188) and 121 Golgi tendon organ capsules per gram (range: 79–166).

Figure 3 shows muscle mass and receptor contents as well as receptor density for left versus right side segmental muscle. The plots show an approximate symmetry of these parameters for a given caudal segment. Dissymetry tended to increase caudal to the 8th segment, as is particularly evident with respect to receptor density. In spite of this fluctuation, the scatter plot analysis (Fig. 4) suggests the essential symmetry of left versus right side muscle mass as well as receptor contents, the slope of the regression line being close to one (0·92 for muscle mass, 0·84 for spindles and 0·83 for Golgi tendon organs). Barker & Chin (1960) have reported similarity between
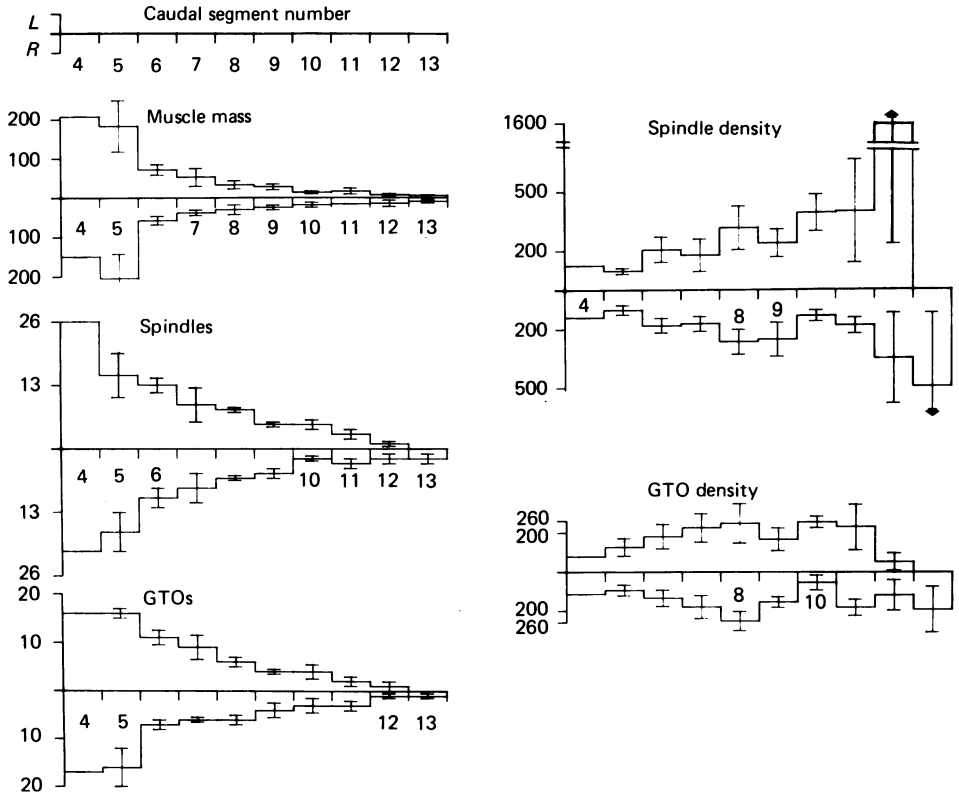
Fig. 3. Average values of segmental data. Caudal segment number given on abscissae. In all graphs, each bin shows the average contents for left (upper half) and right (lower half) side of the segment. Vertical lines indicate the value of the standard deviation, plotted centred on each bin's contents. Segment no. 4 data were obtained for 2 cats only. Compare with Fig. 4. GTO, Golgi tendon organ.

numbers of spindles found in left and right side limb muscles of cat (rectus femoris, tibialis anterior and forelimb Vth interosseus muscles).

Tandem spindles

An average of 25 % (range, 13–30 %) of the total number of spindle capsules were arranged in an end-to-end manner. The observation of intrafusal muscle fibres extending between capsules confirmed such end-to-end arrangements as tandem spindles. Similar values of this 'tandem fraction' (Barker & Ip, 1961) have been reported for other cat muscles (17 % for rectus femoris: Barker & Ip, 1961; 11 % for soleus and 12 % for medial gastrocnemius: Swett & Eldred, 1960a). There was an average of seven (range, 5–11) such arrangements per side, consisting of two (84 %) or three (16 %) capsules. While these values are similar to those found for rectus femoris of cat (Barker & Ip, 1961), only about 2 % of rat tail muscle spindles are in tandem (Thompson, 1970; Andrew, Leslie & Thompson, 1973). In no case did closely adjacent spindle capsules (whether single or a member of a tandem) appear to share intercapsular continuity ('compound' or 'parallel complex': Richmond & Abrahams, 1975) or a common surrounding sheath ('paired linkage': Richmond & Abrahams, 1975), as has been reported in rat tail muscle (Thompson, 1970).
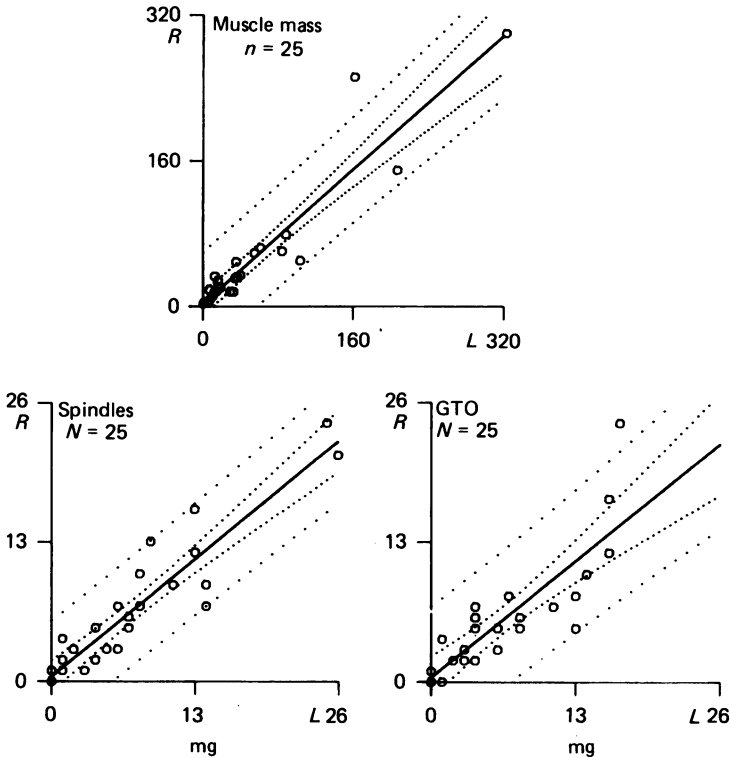
Fig. 4. Scatter plot tests of bilateral symmetry. Left and right side segmental contents shown on the abscissa and ordinate, respectively. Data taken from Fig. 2. Also see Table 1. GTO, Golgi tendon organ.

Ia/Ib afferent axon ratio

An average of 16 % (range: 4–30 %) of the total number of Golgi tendon organ capsules was innervated by an axon which also innervated a second Golgi tendon organ (Fukami, 1980). Each afferent axon branch could be traced centrally from each innervated Golgi tendon organ to a common nodal branch point of the parent axon. Rarely (4 %), the afferent unit included three Golgi tendon organ capsules.

Given the total number of singly or multiply innervated Golgi tendon organs and spindle capsules, estimates were made of the relative number of large myelinated afferent fibres from each whole tail side. Assuming that each spindle capsule had one 'primary' (Ia) afferent ending, the average ipsilateral Ia/Ib afferent axon ratio over the entire length of the tail was estimated to be 1·3 (range: 1·0–1·7: also see Table 1.2, Matthews, 1972). Similarly, the average segmental Ia/Ib fibre ratio was found to be 1·4 (range: 1·0–2·0). The segmental Ia/Ib ratio did not show any systematic change in the rostrocaudal direction.

Capsular dimensions

There was a wide range of capsular sizes, as is shown in the population distributions of Figure 5. The greater uncertainty in precisely measuring the Golgi tendon organ capsular length presumably caused the sharp fall-off in observed numbers of longer Golgi tendon organ capsules. Distributions of Golgi tendon organ and spindle
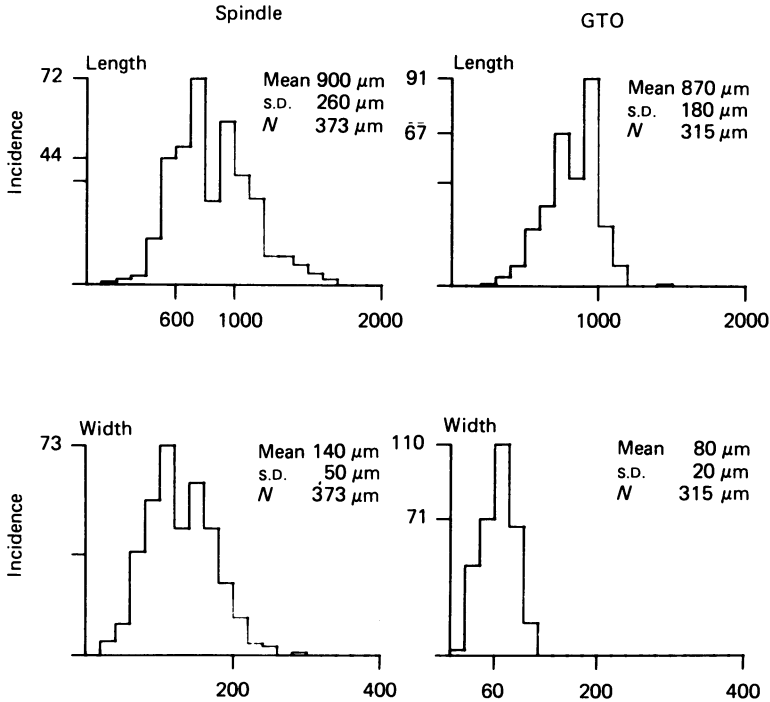
Fig. 5. Histograms of receptor capsule dimensions. Bin widths used for both spindles (left) and Golgi tendon organs (GTO, right) are 100 μm for lengths (upper) and 20 μm for widths (lower).

capsular length overlapped considerably, with estimated mean values ranging from 700 to 1000 μm. By contrast, capsule width distributions were different, with mean values of 100–140 μm for spindles and 60–80 μm for Golgi tendon organs. The capsular lengths of cat tail muscle spindles were generally shorter than those reported for cat rectus femoris (Barker & Ip, 1961) and dorsal neck muscles (Richmond & Abrahams, 1975). Golgi tendon organ capsule widths were similar to those found in certain jaw muscles of cat (Lund et al. 1978).

The possibility of correlation between capsular length and width was studied with scatter plot analysis (Fig. 6; Table 1). The data suggested a correlation between capsular length and width of both spindles and Golgi tendon organs. The considerable amount of variability in the relationships may have been due partly to the uncertainty of the length measurements.

Number of muscle fibres in series with a single Golgi tendon organ

Golgi tendon organ capsules were connected in series with an average of 10 muscle fibres (range: 3–22). Similar values have been reported for other cat muscle Golgi tendon organs (Barker, 1967). The number of muscle fibres inserting into a Golgi tendon organ was significantly correlated with the width of the capsule (Fig. 6; Table 1).
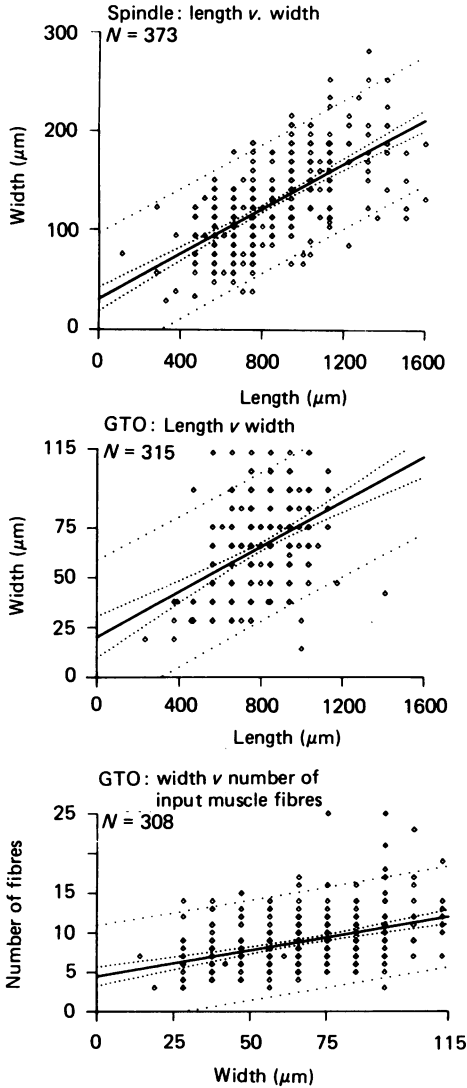
Fig. 6. Scatter plot of capsular size parameters. Muscle spindle (top) and Golgi tendon organ (GTO: middle) lengths and maximum widths were correlated, as were Golgi tendon organ (GTO) width and the number of inserting muscle fibres (bottom). See Table 1. Note that many plotted datum points are superimposed (e.g. middle plot), giving incorrect impression of non-correlation.

Spindle location along the longitudinal axis of extrafusal fibres

Spindle capsules were examined with regard to their location along the length of the extrafusal muscle bundle. The location of each spindle capsule was expressed as a percentage of extrafusal muscle length measured from the tendon to the capsule equator. Some few spindles close to the tendon were located adjacent to a Golgi tendon organ ('dyad': Marchand, Bridgeman, Shumpert & Eldred, 1971), or most rarely (total of 4 cases) in series with a Golgi tendon organ (Fig. 7; Barker, 1948; Marchand *et al.* 1971; Richmond & Abrahams, 1975; Lund *et al.* 1978).
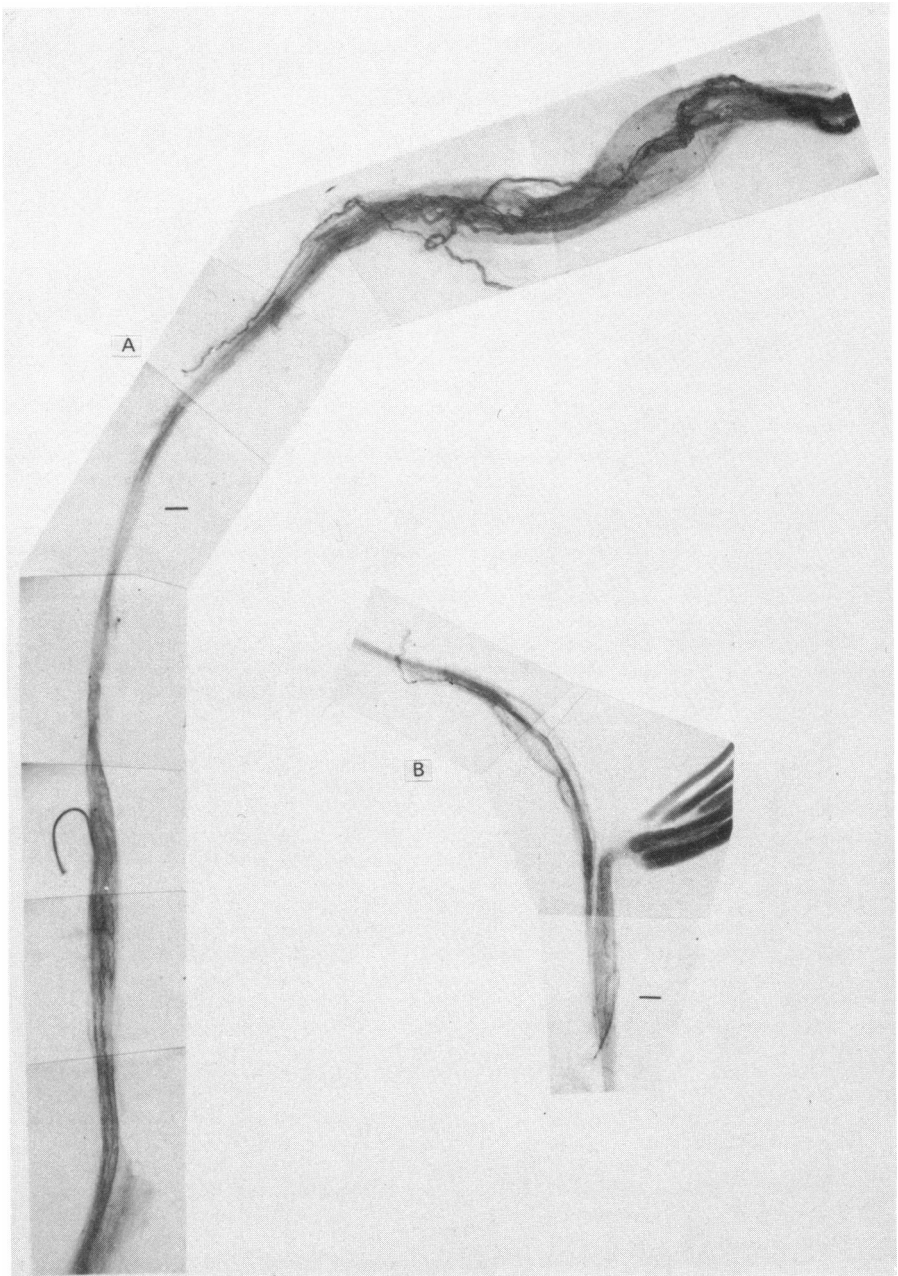
Fig. 7. Examples of OsO$_4$ stained muscle spindles and Golgi tendon organs. (A) A muscle spindle in series with a Golgi tendon organ. (B) A muscle spindle adjacent to Golgi tendon organ (dyad). (C$_1$) Branching of a single afferent axon innervating two Golgi tendon organs. Arrowhead indicates nodal branch point. (C$_2$) Magnified picture of the branching point shown in C$_1$. Nomarski optics. Calibration bar, 100 μm for A, B and C$_1$, and 50 μm for C$_2$.
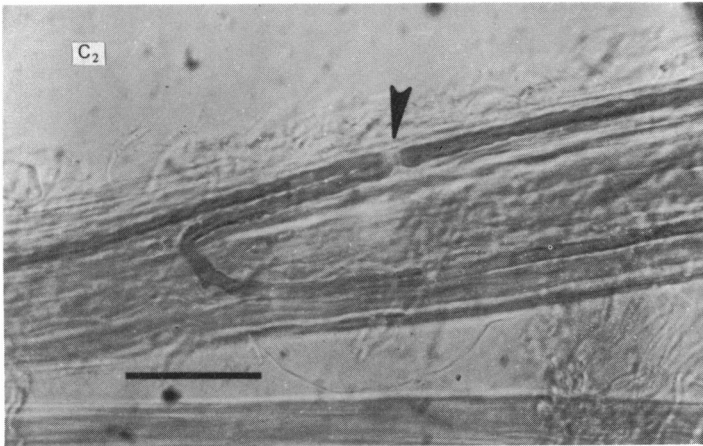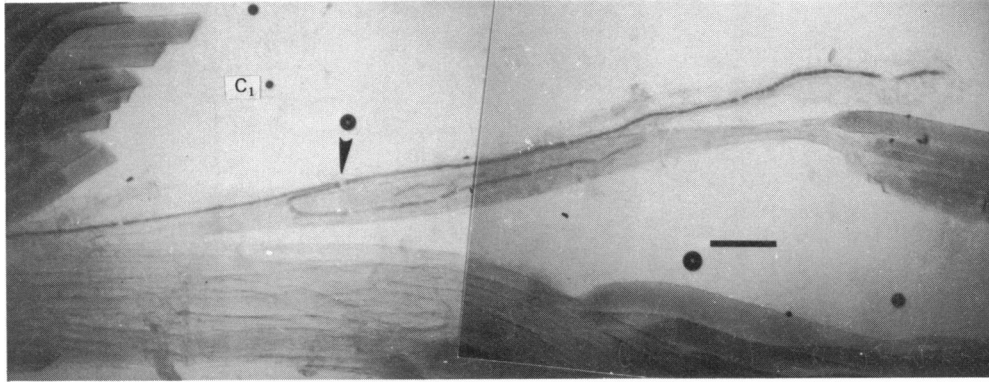
The distribution of spindles along the extrafusal longitudinal axis was not uniform. Whereas nearly equal numbers (29 % of the total) of spindles occurred in each of the first three fourths of the muscle length from the tendon, only 13 % of the total number of spindles occurred over that fourth closest to the periosteal origin, which lacks a tendon.

While there was a correlation between spindle capsular width and position of the equator along the muscle longitudinal axis (Table 1), there was no correlation between spindle capsule length and longitudinal position (Table 1). However, the average capsular length (970 μm) of spindle capsules in the intermediate third was 13 % longer than that of spindles in the proximal or distal thirds (840 and 870 μm, respectively). A similar result (but with 38 % difference for the middle third) was observed for rectus femoris (Barker & Ip, 1961).

A small number of spindles (21/373 or 5·6 %) could be termed 'unipolar' (Barker & Ip, 1961) in that the distal edge of the capsular fusiform enlargement was quite close to (< 300 μm) or attached to the tendon.

DISCUSSION

The present results reveal that the cat tail dorsolateral muscle is richly provided with proprioceptors. Average as well as total spindle densities are among the highest reported for mammalian muscles of fine movement or posture (Barker, 1974;

Richmond & Abrahams, 1975; Bakker & Richmond, 1980). It remains to be determined whether this high spindle density is related to an abundance of histochemically classified slow fibres, as has been demonstrated for certain hindlimb (Swett & Eldred, 1960b; Yellin, 1969) and neck (Richmond & Abrahams, 1975) muscles.

Segmental receptor numbers and muscle mass decline caudally, similar to the decline reported for rat tail by Thompson (1970), but our data suggest that spindle and Golgi tendon organ densities can be fairly constant over several successive caudal segments. The segmental symmetry of left versus right muscle receptor content is comparable to Barker & Chin's finding (1960) that two laterally opposing homonymous muscles have similar proprioceptive equipment.

Previous work on other muscles has shown that spindle capsules tend to be concentrated along the paths of intramuscular nerves (Chin, Cope & Pang, 1962), resulting in, for example, the greater numbers of spindle capsules in the proximal half of rectus femoris muscle (Barker & Chin, 1960). Muscle spindle distribution observed in the adult might imply a pattern of capsule induction during development (Marchand et al. 1971). Non-uniform spindle distribution with respect to extrafusal longitudinal axis may be part of a design principle which minimizes the numbers of spindles occurring near both poles of a muscle where the muscle would be subject to less passive stretch (Gordon, Huxley & Julian, 1966). According to Meyer-Lohmann, Riebold & Robrecht (1974), such spindles tend to have less static sensitivity.

In contrast to the rat tail (Thompson, 1970) and dorsal neck (Richmond & Abrahams, 1975) muscles, we observed no paired (i.e. fused adjacent) and only a few closely adjacent spindle capsules. A spindle–Golgi tendon organ series arrangement (Marchand et al. 1971) suggests a functional coupling between gamma-efferent and I b-afferent activity, given the suggested sensitivity of a single Golgi tendon organ to a single input muscle fibre contraction (Houk & Henneman, 1967; Binder, Kroin, Moore & Stuart, 1977).

The receptor content of the cat tail dorsolateral segmental muscles differs from that reported for the corresponding muscles in rat tail. The latter contains no Golgi tendon organs (cited by Steg (1964) as a personal communication from Ip). By contrast, rat tail-base muscles are more like the cat segmental muscle in containing about equal numbers of spindles and Golgi tendon organs (Gladden, 1969). High spindle densities in rat tail muscles were alluded to by Thompson (1970), but no figures were given. Rat tail muscles contain 1–5 spindles per segment (Steg, 1964; Thompson, 1970; Andrew et al. 1973), as compared with 5–21 capsules per segment in cat tail dorsolateral muscle. In both cases, spindle content and muscle mass declined caudally (Thompson, 1970; Andrew et al. 1973).

The behavioural uses of the cat's tail, e.g. as a balance in locomotion (Romer, 1959), as a rudder during running (cf. Muybridge, 1957) or as an appendage for communication (Necker, 1970), require fine control of contractions of the dorsolateral and other muscles. The high density of muscle spindles in the tail muscle is comparable to those found in other muscles, such as cat lumbricals, extraocular muscles, and soleus, which initiate fine movements (Barker, 1974). The bilateral symmetry of muscle mass and the content of spindles and Golgi tendon organs is consistent with the delicate control of tail position and movement. Although the similar numbers of ipsilateral I a and I b afferent fibres suggest nearly equal excitatory (I a) and inhibitory (I b) proprioceptive input to the control circuitry at the spinal level of ipsilateral motor units, its functional significance is largely unknown (cf. Stuart, Mosher & Gerlach, 1972).

SUMMARY

Using 3 adult cats, distribution, density and size of muscle spindles (total 373) and Golgi tendon organs (total 315) were examined in dorsolateral muscles of the tail stained with osmium tetroxide.

For each whole tail side, the muscle mass and the number of receptors decreased gradually from the base toward the tip. Irrespective of the segmental level, there was a correlation between the numbers of spindle and Golgi tendon organ capsules. Scatter plot analysis of segmental values revealed that the number of Golgi tendon organ capsules approached the number of spindle capsules. Also revealed was the segmental symmetry of left versus right muscle receptor content.

The average ipsilateral receptor densities were 142 spindle capsules/g (range, 92–188) and 121 Golgi tendon organs/g (range, 79–166). An average of 25 % (range 13–30 %) of the total number of spindles was in tandem. An average of 16 % (range, 4–30 %) of the total number of Golgi tendon organs was innervated by an axon which also innervated a second organ. Assuming that each spindle capsule had one primary afferent (Ia) ending, the average ipsilateral Ia/Ib afferent axon ratio was estimated to be 1·3 (range, 1·0–1·7).

Distribution of Golgi tendon organ and spindle capsular lengths overlapped considerably, with estimated mean values ranging from 700 to 1000 μm. By contrast, capsule width distributions were different, with mean values of 100–140 μm for spindles and 60–80 μm for Golgi tendon organs.

The average number of muscle fibres in series with a single Golgi tendon organ (average, 10; range, 3–22) was correlated with capsular width.

The distribution of spindles along the extrafusal longitudinal axis was not uniform. Whereas nearly equal numbers (29 % of the total) of spindles occurred in each of the first three fourths of the muscle length from the tendon, only 13 % of the total number of spindles occurred over that fourth closest to the periosteal origin, which lacks a tendon.

Functional implications of the above findings were discussed.

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