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Internodal length in ventral roots of bovine spinal nerves varies independently of fibre calibre*

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INTRODUCTION

Ranvier (1872) observed that thick fibres of peripheral nerves have longer internodal segments than the thin fibres. Subsequent morphometric studies have supported this observation, indicating a linear relation between internode length and fibre diameter (Schuchardt, 1948; Fullerton, Gilliatt, Lascelles & Morgan-Hughes, 1965; Lascelles & Thomas, 1966; Chopra & Hurwitz, 1967; and many others). Similar results have been obtained for the internodes of central nerve fibres (McDonald & Ohlrich, 1971; Murray & Blakemore, 1980). The concept that internode length relates linearly to fibre diameter is also widely accepted in the neurophysiological literature (Hursh, 1939), serving as a base for biophysical considerations on the conductive properties of nerve fibres (Paintal, 1973, 1978). The existence of such a linear relationship however, is not universally accepted. Non-linear relationships were found by Schuchardt (1947, 1948) and Thomas (1955), being subject to change during growth. Internode length, furthermore, is clearly independent of fibre calibre in regenerated nerves (Vizoso & Young, 1948; Fullerton *et al.* 1965; Lascelles & Thomas, 1966).

The proportions of an internode result from the variation of two parameters, its length and the calibre of the fibre, or its axon. The factors controlling the calibre of the axon are still poorly understood, but there is reason to believe that axon calibre is not directly interdependent with fibre length (Thomas, 1955). The length of the mammalian internode, on the other hand, is known to be determined by body growth, or by elongation of the fibre. This was recognised by Boycott (1904) and has been supported by numerous subsequent studies (Hiscoe, 1947; Schuchardt, 1947; Vizoso & Young, 1948; Thomas & Young, 1949; Vizoso, 1950; Thomas, 1955; Schlaepfer & Myers, 1973).

Spinal nerve roots provide interesting models for studying internode proportions, since the axons of different spinal roots have similar calibres, while the lengths, or the developmental elongations of the roots vary greatly, due to the different growth rates of spinal cord and vertebral column. This so-called 'developmental ascensus' of the spinal cord causes a craniocaudal increase in internode length in human ventral roots (Friede, Meier & Diem, 1981). The present investigation provides data on bovine ventral roots. This species is of interest since the cow, like the horse, does not have a significant developmental ascensus of the spinal cord (Nickel, Schummer & Seiferle, 1975); it is also a species of very large body size. To make comparisons more instructive, some data from a recent review of internode proportions in rat nerves and roots (Friede, 1983) have been included in the present report.

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Table 1. *Configuration of internodes in bovine ventral roots*

Root	Number of fibres	Internode length (μm)	Fibre diameter (μm)	Correlation coefficient	Mean l/d
C2	120	1647±267	22·1±1·9	0·33	75
C6	153	1123± 95	20·9±1·9	0·09	54
T8	130	1547±210	22·2±1·8	0·22	70
S1	164	1042±144	20·7±1·5	0·24	51
S5	122	1850±288	20·6±1·9	0·56	90

MATERIALS AND METHODS

The spinal cords of three cows were obtained from the slaughterhouse of the Institut für Tierzucht of the University of Göttingen. Cow 1 was 8 years old and weighed 608 kg; its cord length, measured from C3, was 138 cm. Cow 2 was 3 years old, weighed 438 kg and had a cord length of 128 cm. Cow 3 was 8 years old, had a weight of 473 kg and a cord length of 133 cm. Tissues were obtained within about 30 minutes of death and were fixed in glutaraldehyde. Every alternate ventral root was harvested. The roots were post-fixed in osmium tetroxide, and single fibres were teased under a stereomicroscope and mounted in glycerin-gelatin. In addition, specimens of roots were embedded in Araldite, and semithin sections were cut with an ultramicrotome. In each teased fibre all well preserved internodes were identified, numbered, and their lengths measured with a Kontron videoplan by tracing the fibre between the two extreme poles of its myelin sheath at the nodal gap. The mean diameter of the fibre was determined from two measurements, one each on either side of the nucleus of the Schwann cell. These measurements were taken from straight portions of the fibre, in which outer and inner surfaces of the myelin sheaths stood out clearly as sharp, parallel, equidistant lines, giving a uniform thickness of the myelin sheath over a length of several micrometres. This criterion was previously found to define the most dependable site for measurement of fibre calibre in rat nerves (Friede, 1983). No measurements were taken at the level of visible clefts of Schmidt-Lanterman or at paranodal bulbs.

Measurements in teased fibres were calibrated by comparing data from the latter with measurements made in semithin sections of Araldite-embedded specimens of the same roots (Table 1). In these sections, the outer circumference of the myelin sheath and the area of thick fibres were measured with the videoplan, for 100 fibres in each of five roots in each animal. These data were expressed in terms of the diameter of circular fibres having the perimeter measured, or as the diameter of circular fibres having the area measured. The difference between these two parameters indicated the degree of non-circularity; expressed as fibre diameter, it amounted to a factor of 0·95, the individual mean values lying between 0·93 and 0·97.

The mean calibres of teased fibres were always greater than those in semithin Araldite sections; on average the ratio was 0·7. This difference was extremely constant among different roots, and the small variations were consistent from one root to another. The mean ratios of the two measurements were 0·67 in C2, 0·70 in C6, 0·71 in T8, 0·70 in S1, and 0·70 in S5, thus differing maximally by 4%. Possibly, such differences were due to sampling, since thick fibres were teased more readily than thin fibres. This interpretation is unlikely, however, considering the great number of measurements taken, the consistency of the data from one sample to the

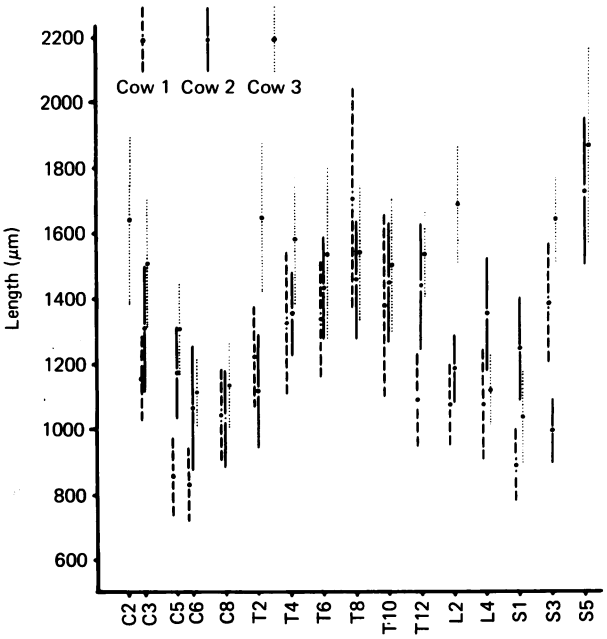

Fig. 1. Segmental variation of internode length showing mean values and standard deviations.

next, and the virtual absence of overlap in the calibres of thick and thin fibres in bovine ventral roots. The ratio of 0·70, therefore, must be attributed to the shrinkage of the fibres during dehydration and Araldite embedding.

RESULTS

Fibre populations of ventral roots

On measuring their diameters, ventral roots have bimodal fibre populations with readily distinguished peaks of thick and thin fibres (Häggqvist, 1948). The thick fibres, innervating the motor units of skeletal muscles, dominate in most segments while the thin fibres are subject to considerable segmental variation. For the pooled segments C2, C6, T8, S1 and S5, the thick fibres had a mean diameter of $21{\cdot}3 \pm 1{\cdot}9\,\mu m$; the thin fibres of the same segments averaged $8{\cdot}7 \pm 1{\cdot}6\,\mu m$ (Fig. 5). For these reasons, data on thick and on thin fibres were treated separately, that on thick fibres forming the main body of this study.

Segmental variations of internode length

Approximately 160 internodes were measured in each ventral root of each animal, yielding a total of 7429 internodes of thick fibres. Histograms of internodal length for each given root of each animal disclosed well defined Gaussian distributions, but there was considerable segmental variation of mean internode length (Table 1). The general pattern of segmental variation is shown in Figure 1. All animals showed the same trend, with the longest internodes in the cervical, thoracic and sacral segments, and relatively short internodes in the lower cervical and lumbosacral segments, the latter corresponding to the origins of the brachial and lumbosacral plexuses. There

Table 2. *Configuration of internodes in ventral roots of the rat (Friede, 1983)*

Root	Number of fibres	Internode length (μm)	Fibre diameter (μm)	Correlation coefficient	Mean *l/d*
C8	44	929±180	13·6±2·6	−0·49	73
T4	45	797±242	12·0±2·0	0·10	62
T11	45	715±125	14·7±2·5	0·30	50
L2	45	1051±138	15·5±1·9	0·47	69
L4	45	1038±191	14·1±2·7	0·12	75
L6	45	1338±228	13·9±1·6	−0·72	98
S3	44	1327±310	13·3±2·3	−0·28	105

was little individual variation in internode length from one animal to another: only segments T2 and L2 had longer internodes, in cow 3.

Maximum internode length

There is consensus among neurobiological investigators that mammalian internodes are rarely longer than 2 mm. Yet there are no specific studies which define the upper limits of internode length. In the present material, in which 7429 internodes were measured, 139 were longer than 2 mm; of these 65 measured between 2000 and 2100 μm, 37 between 2100 and 2200 μm, 15 between 2200 and 2300 μm, and 14 between 2300 and 2400 μm. Only five internodes measured between 2400 and 2500 μm, one measured 2510 μm, one 2672 μm and one 2847 μm. For practical purposes, 2400 μm was the upper limit for internode length and only a rare, excessively long internode exceeded that value. The low absolute frequency of 2% internodes which exceeded 2 mm was somewhat misleading, as 58% of the 139 'long' internodes were obtained from the roots of T8 and S5, in which long internodes were common. Most of the other roots had shorter internodes, substantially below 2 mm in length.

These figures may be compared with the internode length in rat ventral roots (Table 2), obtained with the same technique (Friede, 1983). The longest internode found in the rat was 2120 μm. Generally, ventral root internodes tended to be shorter in the rat than in the cow, on average by approximately 28%.

Relation between internode length and fibre diameter

The relationship between internode length and fibre calibre was determined for five roots including the three roots with the greatest internode length (C2, T8 and S5), and the two with the smallest length (C6 and S1). These five roots had essentially the same mean fibre diameter, but mean internode length differed significantly (Table 1). When internode length was plotted against fibre calibre, the segments C1 and S1 showed virtually no increase of internode length with fibre calibre. For the other segments, internode length tended to increase with fibre calibre (Fig. 2), but there was a great deal of scatter in the results, and the correlation coefficients were quite low (Table 1), similar to those for the rat (Table 2).

The ill-defined relationship of internode length to fibre calibre in some of the roots was obliterated when the data for all five roots were pooled (Fig. 3). There was no correlation at all between internode length and fibre diameter.

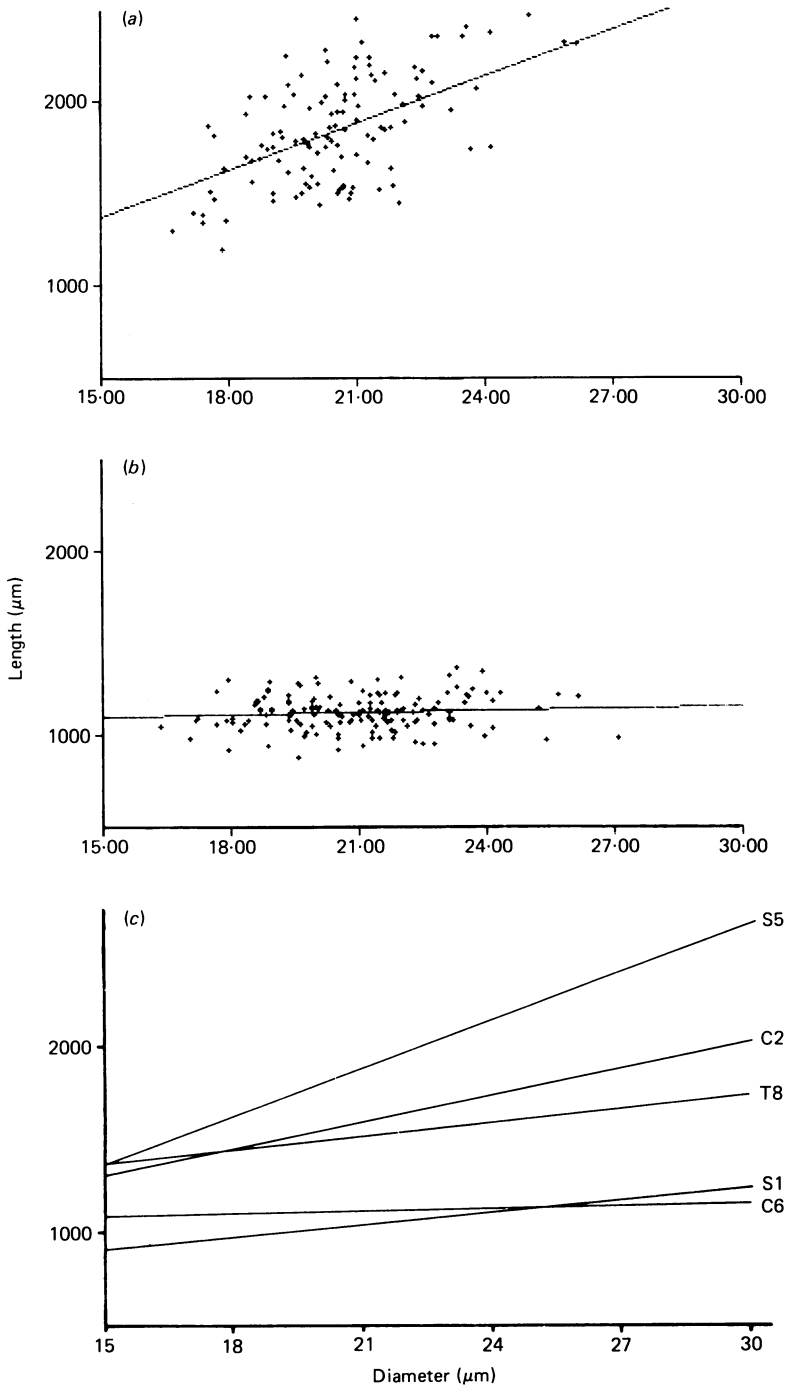

Fig. 2 (*a* -*c*). Relationship of internode length and fibre calibre for S5 (*a*), C6 (*b*) and the regression lines for five different roots (*c*).

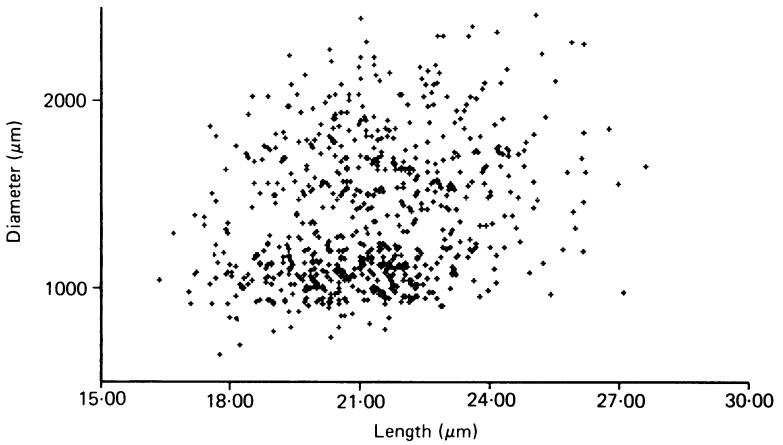

Fig. 3. Pooling of data from five roots shows no correlation between internode length and fibre calibre. The correlation coefficient is 0·26.

Internode configuration

The length of an internode has only limited meaning as a biological parameter, unless compared with fibre calibre: an internode with a length of 1·5 mm is quite long for a thin fibre, while it is standard for a thick fibre. The characteristics of a given internode population are described best in terms of the quotient internode length/fibre diameter (l/d). The value of l/d of a given fibre population may be determined predominantly either by the variance in axon calibre or by the variance in internode length, or by both. For bovine ventral roots, fibre calibres were nearly constant, while internode length varied considerably (Table 1). Accordingly, if the quotient l/d of individual internodes was plotted against internode length, linear relationship with little scatter was obtained for all the five segments studied (Fig. 4). Conversely, if l/d was plotted against fibre diameter, there was considerable scatter (Fig. 4). This relationship is not as self-evident as it may seem from the present data on roots, as some peripheral nerves have exactly opposite variations of internode length and of fibre diameter.

The findings in bovine ventral roots were similar to those for rat ventral roots, where fibre calibre was also rather constant, while internode length and fibre calibre were lower in the rat than in the cow; the proportions of ventral root internodes were similar with values of l/d ranging between 50 and 105 (Tables 1, 2).

Thin myelinated fibres

The density of thin myelinated fibres of spinal nerve roots varied considerably along the spinal cord. Thin fibres comprised a small fraction of the total fibre population in the segments C3 to C8 and in L3 and S5. They were abundant between T2 and L2, where they were arranged in small fields forming a mosaic amongst the population of thick fibres. This segmental pattern indicated that most of the thin fibres in the roots from C8 to L3 were sympathetic nerves. Thin fibres, therefore, were treated as a separate fibre population, having no overlap in histograms which classified fibres either by calibre or by internode length. Fewer thin fibres were available for measurement, partly due to their segmental variation, and also because it was more difficult to tease them.

Segmental variation in the length of internodes of thin fibres was slight, with only

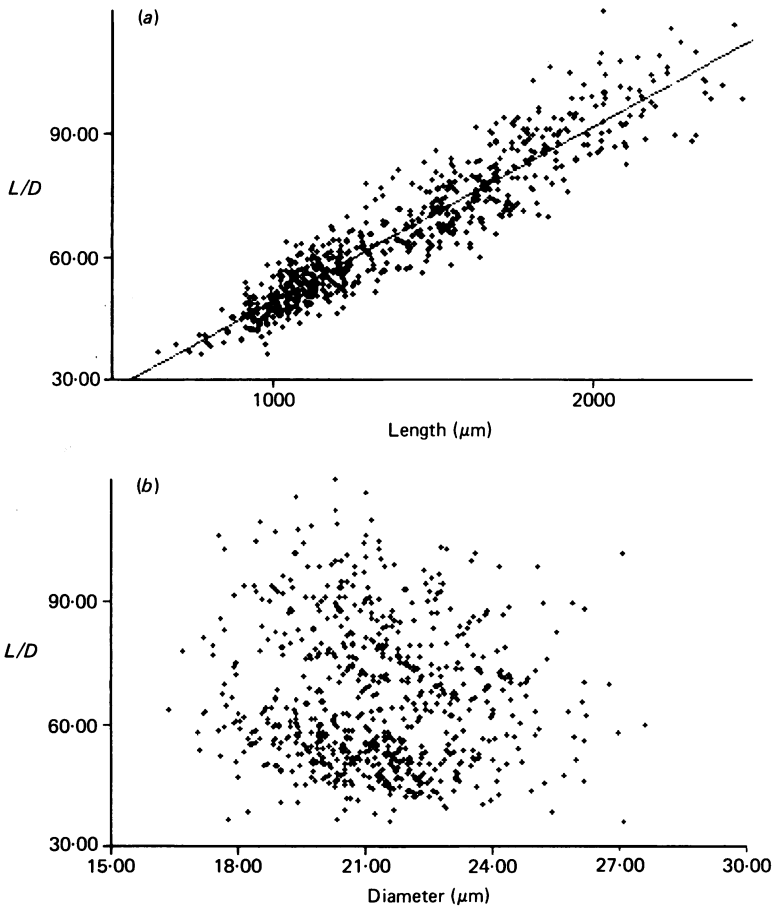

Fig. 4 (*a–b*). The quotient l/d is the product of independent variations of fibre calibre (d) and internode length (l). Whether l/d of a fibre population depends more on variation in d or in l may be estimated by plotting l/d against either l (in Fig. 4*a*) or d (in Fig. 4*b*). In bovine ventral roots, the shape of internodes closely follows variation in internode length: (*a*: correlation coefficient 0·94), independently of fibre calibre (*b*: correlation coefficient −0·069).

a hint of the pattern observed for thick fibres. Slightly shorter internodes prevailed in the segments of the cervicothoracic junction and the lumbosacral segments, but the differences were not statistically significant. Internode proportions were determined for the same five segments as for thick fibres, giving a total of 166 fibres. Thin fibres had shorter internodes than the thick fibres, with a mean length of 702 ± 168 μm for all five pooled segments. The mean diameter of these fibres was $8{\cdot}7 \pm 1{\cdot}6$ μm, and the l/d quotient averaged 80. The latter value was consistent with the observation that thin fibres generally tend to have higher l/d quotients than thick fibres (Friede, 1983), but the difference was relatively small for bovine ventral roots. When internode length of thin fibres was plotted against fibre diameter, there was a vague indication that internode length tended to increase with fibre diameter, but the correlation coefficient was only 0·29. If plots were made for thin and thick fibres combined, there were two clusters of points, which did not lend themselves to regression analysis (Fig. 5); the correlation coefficient for the cluster of thick fibres was 0·26, that for the thin fibres 0·29.

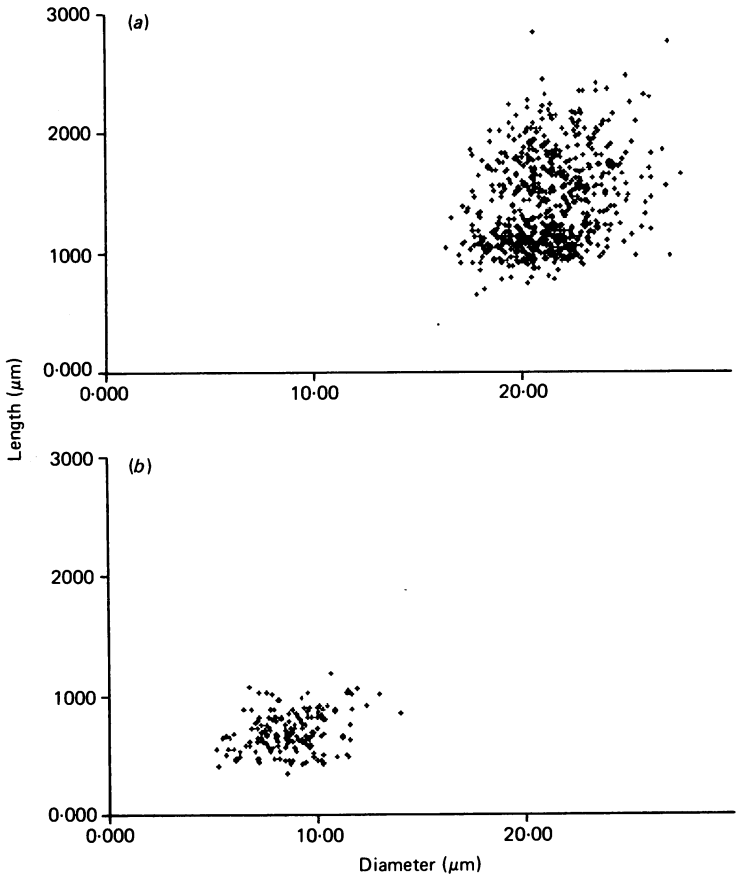

Fig. 5. (*a–b*). Relationships of internode length and fibre diameter plotted separately for the thick (*a*) and the thin (*b*) fibres of five roots (for correlation coefficients see text).

DISCUSSION

The present data add to a growing body of evidence indicating that the length of internodes is quite independent of fibre calibre. The thick fibres of different bovine ventral roots have nearly the same calibre, but the length of their internodes varies considerably from one root to the other. If internodes from several roots are pooled, there is no correlation whatever between internode length and fibre calibre. Thin fibres, moreover, evidently comprise a separate fibre population; most of them are sympathetic nerves (Sheehan, 1941), consistent with their high content of acetylcholinesterase (Gruber & Zenker, 1973; Zenker, Stelzig, Sulzgruber & Neumann, 1979). In addition to these, the gamma-fibres innervating muscle spindles also contribute to the thin fibre population: In the cat gastrocnemius, for example, they comprise 27 % of the total motor fibre population (Hagbarth & Wohlfart, 1952). Sufficient attention needs to be given to the heterogeneity of thin fibres in pathology; for example, the well known differences in vulnerability of thin and thick fibres in amyotrophic lateral sclerosis (Wohlfart & Swank, 1941; Kawamura *et al.* 1981; Sobue *et al.* 1981; Hanyu, Oguchi, Yanagisawa & Tsukagoshi, 1982).

At first sight the data obtained in the present study seem to contradict the many reports indicating a linear relationship between internode length and fibre calibre.

A more thorough understanding of the developmental processes involved in internode geometry may explain these apparent contradictions. Mammalian internode length is determined by the degree of elongation of the fibre subsequent to the onset of myelination. For the fibre population of a given peripheral nerve, those fibres destined to become the thickest fibres myelinate earlier than those destined to become thin fibres. This is also true for ventral roots of spinal nerves (Rexed, 1944). If the myelination period were long enough to allow the time of onset of myelination of each given fibre to anticipate its definitive calibre, all internodes would elongate in strict relationship to increases in calibre, resulting in identical proportions of internode length and fibre diameter for all adult internodes. In reality, however, myelination periods are much shorter, so that the l/d quotient of thin fibres is generally higher than that of thicker fibres in any given nerve (Friede, 1983). Moreover, the growth of a given nerve may not be uniform along its length, so that differences in internode length may develop along one and the same fibre (Vizoso, 1950). For example, in the facial nerve of the rat the l/d quotient of a fibre 10 μm in diameter is 47 in the intraosseous portion within the petrous temporal bone, but is 74 in its branches in the face (Friede, 1983). These observations explain why internode length may increase linearly with fibre calibre at a given level in a given nerve, even though the two factors are actually independent of each other (Thomas, 1955).

On comparing the proportions of internodes in ventral roots of the cow and the rat, the cow has somewhat longer internodes than the rat; the cow also has somewhat thicker fibres. As a result, the rat and the cow have similar l/d factors in their ventral roots, and the impression may be obtained, therefore, that there is a tendency to keep the l/d quotient constant. This similarity between species is just as coincidental as the linear relationship of internode length and fibre calibre seen in a given peripheral nerve. If l/d of rat ventral roots is compared with l/d of many peripheral nerves in the rat, variance (for 10 μm diameter fibres) ranges between 18 in the acoustic nerve, for example, and 135 for the 3rd sacral root. Clearly, there is no biological trend to confine the l/d quotient within a narrow limit.

Another question concerns the upper limits of internode length. If all internodes grew in proportion to body size, larger species would have enormously long internodes, imposing excessive strain upon the metabolic resources of the Schwann cell (Friede & Bischhausen, 1980). A search for extremely long internodes in the present material shows an upper range of internode length above the commonly accepted upper limit of 2 mm, i.e. 2·4 mm. Only an exceptional internode may become longer, and the longest found in this study is 2847 μm. Yet such data may not necessarily indicate limits to cell growth. Maximum length of internodes may simply be the consequence of a relatively uniform developmental timing of the myelination period in different species (Schlaepfer & Myers, 1973). If myelination were timed to occur at a stage of development when the fibre population had attained about one eighth of its definitive length, there would be a fairly constant value for mature internode length in all species (Friede *et al.* 1981).

The absence of a correlation between internode length and fibre calibre in bovine ventral roots agrees with similar findings in man, where internode length varies in proportion with root growth, independent of fibre calibre (Friede *et al.* 1981). However, the variance in internode length along the successive roots of the spinal cord differs greatly between the cow and man. In man, and also in the rat, the growth rate of the vertebral column greatly exceeds that of the cord, resulting in a

marked 'developmental ascensus' of the cord causing craniocaudal differences in the elongation of roots with maximal elongation of the lumbosacral segments. The development of the spine of the cow differs from man in that the lower cervical and the upper lumbosacral segments, from which the limb plexuses originate, remain exactly opposite their corresponding intervertebral foramina. The cow, like the horse, has practically no ascensus of the spinal cord (Nickel *et al.* 1975), apart from foreshortening of the sacral segments in the conus medullaris. The latter correlates with a minor increase in internode length in the bovine lumbosacral segments, compared with the very marked increase found in man. The fluctuations in internode length along the bovine thoracic cord presumably reflect variation in segmental length relative to the distance between intervertebral foraminae. Generally, therefore, the patterns of root internode length in different species tend to correspond to the degree of developmental displacement of the spinal cord segments relative to the vertebral column, which is characteristic of that species.

SUMMARY

The length of internodes in bovine ventral spinal nerve root fibres varies in an irregular pattern along the spinal cord with short internodes for the cervicothoracic and lumbosacral segments, and long internodes for the high cervical, thoracic and sacral segments. This pattern of variation is independent of axon calibre, which is fairly constant between roots. The data show that internode length and fibre calibre vary independently of each other, resulting in internodes of different proportions (length/diameter quotient) for different roots. Maximum internode length was determined at approximately 2400 μm; the longest internode found measured 2847 μm.

The segmental variance in ventral root internode length in the cow differs from that in man or rat, which show a craniocaudal increase in internode length. These species-dependent differences relate to differences in the degree of the 'developmental ascensus' of the spinal cord.

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