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The number and distribution of muscle spindles in human intrinsic postvertebral muscles

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INTRODUCTION

Analyses of human patterns of movement have shown that a large number of daily activities require movement of the head and trunk as a basic component. The control of postvertebral muscles is obviously of importance in these movements as well as in the maintenance of posture, particularly that of the head.

Electromyographic evidence in subjects studied by Zuk (1962), Hoogmartens & Basmajian (1973), Monticelli, Ascani, Salsano & Salsano (1975) and Hoogmartens & Stuyck (1977) shows that asymmetry of stretch reflexes in spinal muscles may play a part in the causation and progression of many cases of idiopathic scoliosis. Spencer & Eccles (1976), Spencer & Zorab (1976) and Spencer (1977) have produced morphological and histochemical evidence to show that there are relatively more tonic (Type I) fibres on the convex side of the scoliotic curve than on the concave side, although it is not clear from their report whether this asymmetry in the distribution of muscle fibre types is a predisposing factor or a result of idiopathic scoliosis. Nevertheless, earlier work by Cooper (1960, 1966) showed that long, complex spindles were particularly numerous in tonic muscles.

Bartelink (1955), Davis (1956*a*, *b*) and Kumar (1971) have noted that postvertebral muscular activity is correlated with variations in intra-abdominal and intrathoracic pressures whilst lifting weights from the stooped position. Kumar & Davis (1973) postulated that receptors in the erector spinae complex might play a significant role in controlling these variations in intratruncal pressures.

Because of the possible involvement of the postvertebral muscles in these intricate functions of the body, their patterns of innervation and control need to be clarified. Detailed information of motor supply is scanty, and attempts to determine segmental distributions have not been encouraging. The literature on the incidence of sensory receptors, including muscle spindles, is incomplete.

Gregor (1904) reported on a quantitative study of muscle spindles in some intrinsic postvertebral muscles of a 26 cm human fetus, but his specimen was incomplete. Detailed quantitative studies of human muscle spindles have also been made by Voss (1956) in anterior muscles of the neck, trapezius and latissimus dorsi; by Voss (1958, 1959) in suboccipital and ventral abdominal muscles, and by Cooper & Daniel (1963) in suboccipital muscles. Cooper (1960, 1966) summarised an extensive series of reports by Voss and his co-workers on the distribution of spindles in human limb, trunk and cranial muscles. There appears to be no information on the segmental distribution of muscle spindles in the posterior muscles of the trunk.

The present study is mainly concerned with the number and distribution of muscle spindles.

MATERIALS AND METHODS

The study is based on a 21 weeks old human fetus (C.R. 180 mm) in which the gross form of all muscles was fully established. Evidence provided by Cuajunco (1940, 1942) and Bowden (1963) suggests that by this age there would be a full complement of well formed spindles, although the bulk of tissue would be far less than in the adult. The vertebral bodies and intervertebral discs of this 21 weeks old specimen were easily identifiable and sufficiently developed to demarcate the vertebrae from one another.

The fetus was fixed by perfusion through the umbilical vein, with Fitzgerald–Richardson fixative, and stored for some days in the same fixative. The skin and superficial (dorsohumeral) muscles were dissected out to expose the posterior layer of thoracolumbar fascia. The vertebral column with all the intrinsic postvertebral muscles *in situ* was then separated from the rest of the body by careful dissection, and divided with a sharp scalpel into segments by cutting through intervertebral discs between successive vertebrae from C2 to S4. C1 and C2 were separated by dividing the dens between the two vertebrae and disarticulating the posterior atlanto-axial joint. These stages were crucial and care was taken to avoid loss of tissue that would affect subsequent reconstruction. The cephalic end of each segment was marked with indelible ink for orientation during embedding and sectioning. The segments were also labelled serially according to their respective vertebral levels. Because all segments contained skeletal elements, it was necessary to decalcify them before processing. Bensley's fluid was used for this purpose. Complete decalcification of all blocks was achieved within 48 hours. The decalcified specimens were processed in ascending grades of alcohols, cleared in xylene, vacuum-impregnated and embedded in paramat, in such a way that the cephalic end of each block would be cut first during sectioning. The spines, ligamentum nuchae and interspinous ligaments were chosen as intrinsic reference marks, since these maintained a constant relationship to the rest of the block. Serial 10 μm sections were cut and every section was mounted, the orientation being standardised. A note was made of any sections that were damaged and discarded in cutting and appropriate blank spaces were left on the slides, so that accuracy could be maintained during serial reconstruction.

Successive slides were stained with iron haematoxylin and eosin, Van Gieson's stain with Weigert's haematoxylin; and Glees' silver impregnation technique respectively.

Sections were systematically examined using a binocular Nikon (Ske II) microscope. General morphological features and the presence and distribution of spindles were noted. The positions of spindles in every fifteenth section were plotted on isometric paper. Spindles were identified by their capsules and equatorial regions. These were followed as far proximally and distally as possible. Only the equatorial regions were used for counting.

Plotting of spindles

Isometric paper (C 82B, Entwistle Thorpe) (Fig. 1 *a*) was used as the development sheet. The grid was prepared by drawing a vertical reference line along the *x* axis,

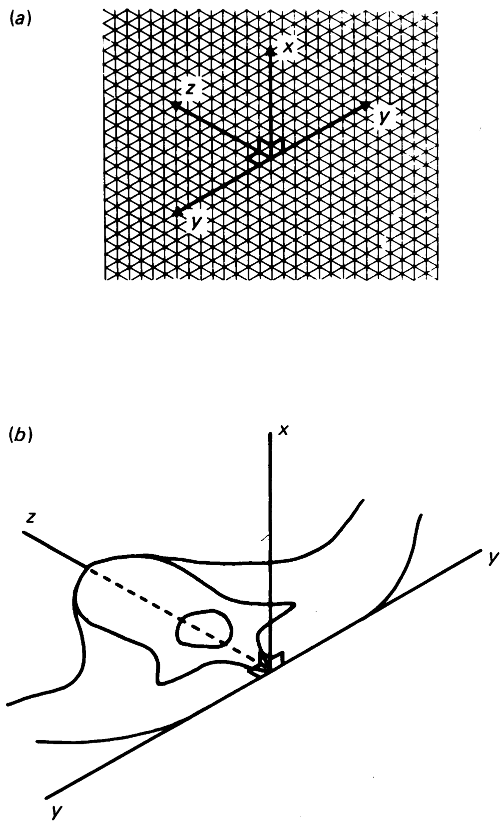

Fig. 1. (*a*) Diagram showing the orientation of the x, y and z axes on the isometric paper. (*b*) Diagram showing the orientation of the outline of the tissue section on the isometric paper in relation to the x, y and z axes.

in the middle of the sheet. A series of horizontal lines was then drawn along the y axis to intersect the reference line at arbitrarily selected intervals.

In order to accurately localise tissue elements, the intersection of a cross line graticule incorporated in one of the eyepieces of the microscope was used as a reference point.

The (intrinsic) reference mark of the tissue was first aligned with the reference point of the graticule and the corresponding coordinates were read off the stage micrometer. These were plotted on the grid to coincide with the intersection of x, y and z axes. The scale for the y and z axes was then calibrated against that of the reference mark.

Other points on the outer limits of the section were then aligned in turn with the reference point and the coordinates obtained were plotted on the grid. All points so plotted were joined to give the outline of the tissue (Fig. 1 *b*).

Next, the positions of all spindles seen in every fifteenth section were plotted on the development sheet, using coordinates obtained according to the technique described for the tissue outline. The point for the spindles automatically fell within the outline of the section. Each slide was examined twice, the second scanning serving as a check on the first.

Corresponding spindle points from consecutive charts were joined by straight

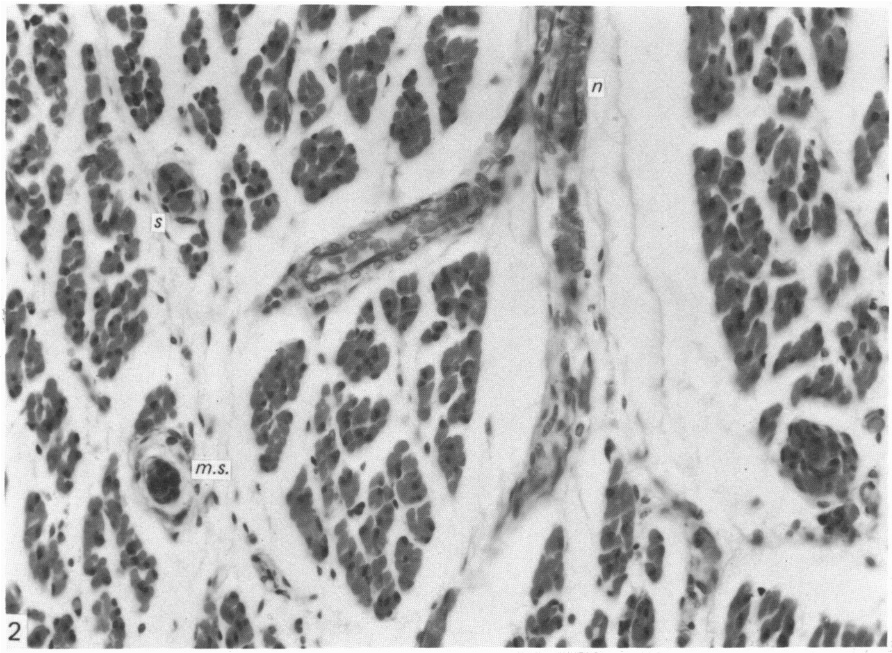

Fig. 2. Photomicrograph taken from an iliocostalis lumborum muscle showing the equatorial region of a muscle spindle (*m.s.*). The polar end of the capsule of another spindle (*s*) is visible. The picture also shows a neurovascular bundle (*n*) branching to supply the spindles. Note the relative absence of interfascicular connective tissue in this 21 weeks old specimen. Haematoxylin and eosin. ×250.

lines along the x axis to give projection charts. In reconstructing projections of spindles, reference was made to the original slides whenever necessary. It was therefore possible to identify spindles in consecutive charts.

OBSERVATIONS

Muscle spindles were seen and counted on both the left and right sides in the cervical, thoracic, lumbar and sacral parts of the intrinsic postvertebral muscles. They were very conspicuous and appeared well developed (Fig. 2). Compound spindles were present in all groups. The majority of these consisted of a pair of spindles lying in parallel and sharing a capsule; in the cervical region, compound spindles containing three or four spindles were found. Some tandem spindles were also seen, but because of the absence of corroborative evidence of the occurrence of a serial arrangement of sensory innervation, no separate counts of tandems were made.

Counts of muscle spindles

A total of 1650 spindles were counted on the left side of the body. Of these, 610 were found in the medial column of muscles whilst the intermediate and lateral columns contained 735 and 305 spindles, respectively. On the right side, there were 1634 spindles, of which 606 were in the medial column and 742 and 286 were located in the intermediate and lateral columns, respectively (Table 1). Spindles in compound arrangements were counted as discrete units in working out the total spindle counts. The number of compound spindles counted in the various columns is compared with the total spindle counts in Table 2.

Table 1. *The number of muscle spindles in the postvertebral muscles*

Segmental level	Semispinalis muscle		Medial column spinalis and multifidus muscles		Total		Intermediate column longissimus capitis and cervicis muscles		Lateral column iliocostocervicalis muscle		Total of all columns	
	L	R	L	R	L	R	L	R	L	R	L	R
C 1	27	23	—	—	27	23	5	4	—	—	32	27
2	21	20	4	3	25	23	14	10	—	—	39	33
3	17	21	9	10	26	31	15	11	—	—	41	42
4	23	23	23	21	46	44	21	20	—	—	67	64
5	23	21	13	13	36	34	19	24	—	—	55	58
6	22	16	13	11	35	27	23	24	—	—	58	51
7	18	16	11	12	29	28	16	12	2	5	47	45
T 1	—	—	—	—	18	18	30	28	22	21	70	67
2	—	—	—	—	20	18	42	43	27	25	89	86
3	—	—	—	—	23	21	32	36	19	14	74	71
4	—	—	—	—	13	17	27	33	19	19	59	69
5	—	—	—	—	21	21	39	37	19	20	79	78
6	—	—	—	—	21	21	37	33	22	22	80	76
7	—	—	—	—	17	19	30	32	13	14	60	65
8	—	—	—	—	20	20	30	32	19	16	69	68
9	—	—	—	—	15	18	25	27	15	12	55	57
10	—	—	—	—	14	21	32	34	15	17	61	72
11	—	—	—	—	20	20	32	33	14	13	66	66
12	—	—	—	—	25	18	49	49	26	23	100	90
L 1	—	—	—	—	19	23	53	58	27	19	99	100
2	—	—	—	—	29	21	51	56	27	27	107	104
3	—	—	—	—	23	25	38	33	19	19	80	77
4	—	—	—	—	34	33	39	44	—	—	73	77
5	—	—	—	—	15	25	36	29	—	—	51	54
S 1	—	—	—	—	23	23	—	—	—	—	23	23
2	—	—	—	—	16	14	—	—	—	—	16	14
Total number of spindles					610	606	735	742	305	286	1650	1634

Table 2. *The proportion of compound spindles in the postvertebral muscles*

	No. of compound spindles	Total no. of spindles	Percentage compound spindles
		Medial column	
Left	54	610	8·85
Right	55	606	9·08
		Intermediate column	
Left	70	735	9·52
Right	76	742	10·24
		Lateral column	
Left	27	305	8·85
Right	31	286	10·84

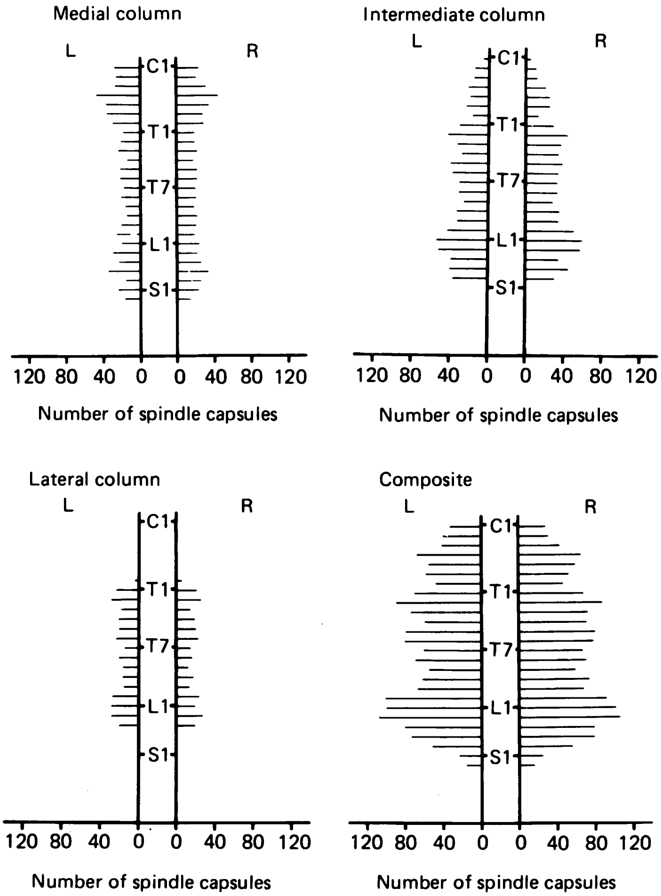

Fig. 3. Bar graphs showing the number of muscle spindles counted at each segmental level in medial, intermediate and lateral columns of the intrinsic postvertebral muscles. The composite graph represents the total number of spindles at each level (i.e. medial, intermediate and lateral columns together). L and R indicate the left and right sides of the body, respectively.

Table 3. *Distance of spindles from the mid-line* (*mm*)

	Cervical	Upper thoracic T1–T4	Mid-thoracic T5–T8	Lower thoracic T9–T12	Lumbar	Sacral
			Left			
Spread from mid-line	0–13	0–11	0–13	0–13	0–13	1–6
Peaks	7–9	4–4	3–4	6–7	6–7	2–3
		9–10	7–8			
			10–11			
			Right			
Spread from mid-line	0–13	0–11	0–13	0–13	0–13	1–6
Peaks	7–9	3–4	3–4	5–6	5–6	2–3
		9–10	7–8			
			10–11			

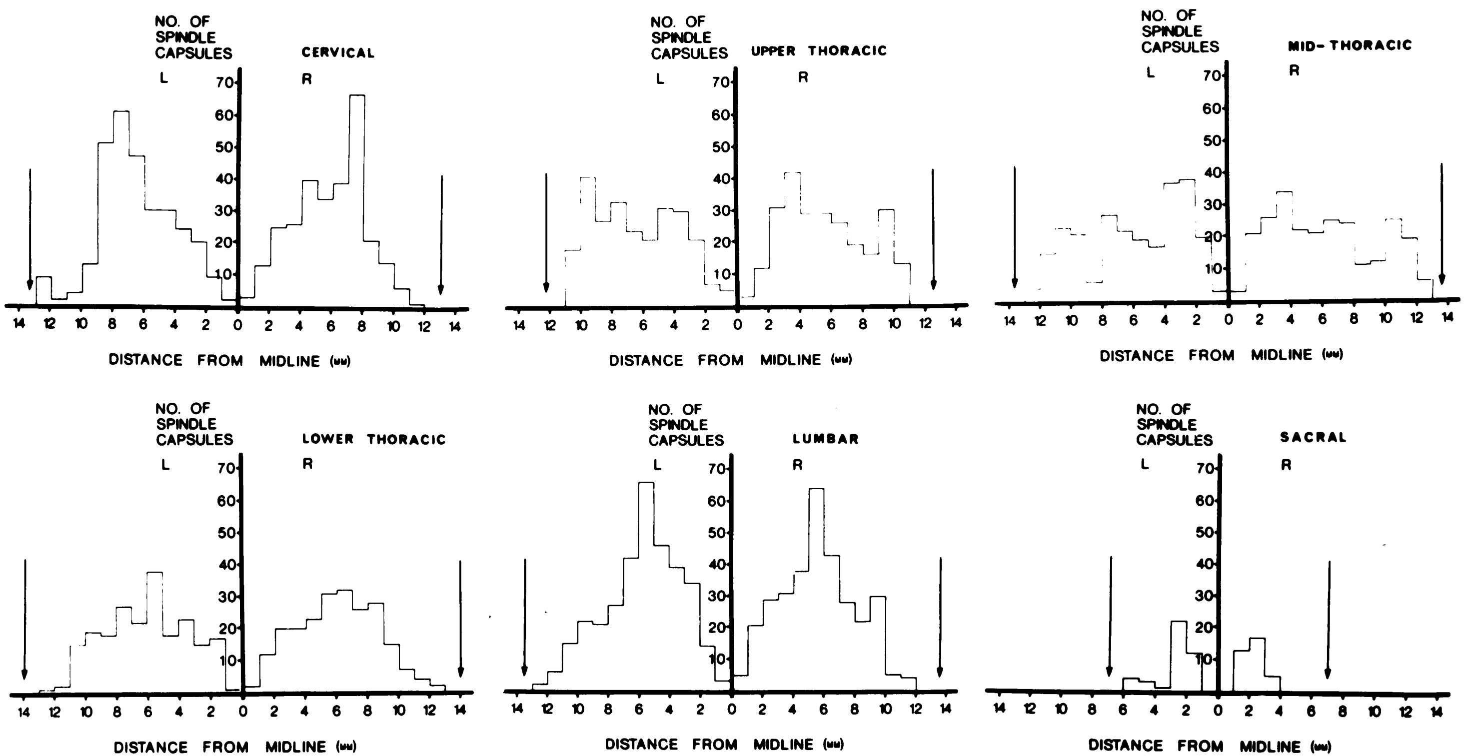

Fig. 4. Histograms showing the spread of spindles from the mid-line in the coronal plane. The neck and trunk were subdivided for this purpose into (*a*) cervical; (*b*) upper thoracic; (*c*) mid-thoracic, T5–T8; (*d*) lower thoracic, T9–T12; (*e*) lumbar and (*f*) sacral, to illustrate difference in spindle distribution. Arrows indicate the lateral limits of the muscles.

Table 4. *Depth of spindles: cervical region (mm)*

	Semispinalis muscle		Spinales and multifidus muscles		Longissimus capitis and cervicis muscles	
	Depth	Peak	Depth	Peak	Depth	Peak
Left	0–2·8	0·2–0·4	1·6–1·8	—	0–3·8	0·4
			2·4–2·6	—		
			3·2–3·4	—		
Right	0–2·8	0·2–0·4	1·6–1·8	—	0–3·6	0·4
			2·4–2·6	—		
			3·2–3·4	—		

Table 5. *Depth of spindles: thoracic region (mm)*

	Medial column		Intermediate column		Lateral column	
	Depth	Peak	Depth	Peak	Depth	Peak
Left						
Upper thoracic	0–2·2	0·4–0·6	0–2·8	0·2–0·8	0–1·6	0·2–0·8
		1·4–1·6				
Mid-thoracic	0–2·2	0·2–0·4	0–3·0	0·2–1·2	0–1·4	0·2–0·6
		1·2–1·4				
		1·8–2·0				
Lower thoracic	0–2·2	0·6–0·8	0–3·2	0·2–1·2	0–1·2	0·2–0·4
Right						
Upper thoracic	0–2·4	0·2–0·4	0–2·4	0·2–0·8	0–1·6	0·2–0·8
		1·2–1·4				
Mid-thoracic	0–2·2	0·2–0·4	0–3·0	0·2–1·2	0–1·4	0·2–0·6
Lower thoracic	0–3·0	0·6–0·8	0–3·8	0·2–1·2	0–1·2	0·2–0·4

Comparison of the absolute number of spindles in the various regions

In the neck, more spindles were found in the medial column (semispinalis, spinalis and multifidus muscles) than in the intermediate and lateral columns (Fig. 3). A marked increase in the spindle content of the medial column was seen in the mid-cervical region (C4) whilst the intermediate column showed only a small rise. Throughout the thoracic and lumbar regions (T1–L5), the intermediate column had more spindles than the lateral and medial columns, which appeared to have similar counts. All groups generally showed an increase in the absolute numbers of spindles in the lumbar region.

The number of spindles at the junctional zones

The mechanics of the transitional zones are of great interest and their relative spindle contents might be considered as a measure of the degree of monitoring and neural regulation occurring across the joints.

Table 6. *Depth of spindles: lumbar region (mm)*

	Depth	Peak
	Medial column	
Left	0–3·2	0·6–0·8
Right	0–3·2	0·6–0·8
	Intermediate column	
Left	0–4·4	0·4
Right	0–4·2	0·6
	Lateral column	
Left	0–4·6	0·4–0·8
Right	0–4·6	0·4–0·8

At the cervicothoracic junction, there was an increase in the number of spindles in all three columns of muscles which was most marked in the intermediate column.

At the thoracolumbar junction, an increase in the number of spindles was seen in all three columns, the intermediate column showing the highest numbers.

The steady decrease of spindle counts occurring in the lower lumbar region continued across the lumbosacral junction. Because of regional differences in the bulk of muscles, valid comparisons of spindle populations can be made only if the relative weights or volumes of the muscles are known.

Distribution of spindles within the postvertebral muscles

Muscle spindles were found at all levels and showed considerable overlap. However, because the details of entry and the intramuscular branching of the nerves supplying these muscles are not known, it was difficult to correlate spindle distribution of nerve supply. Nevertheless, most of the spindles were noted as located near neurovascular bundles.

Distance from mid-line

Table 3 presents an analysis of the regional distribution of spindles in the various columns.

Because the topography of the postvertebral muscles is known, it is possible to determine which muscle groups have the highest concentration of muscle spindles.

Histograms of the lateral spread of muscle spindles from the mid-line are given in Figure 4. The peak observed in the cervical region coincided with the position of the semispinalis muscles. In the upper thoracic region (T1–T4), the medial peaks were higher than the lateral ones, and were produced by spindles in the spinalis, semispinalis, multifidus and longissimus muscles. The lateral peak was produced by spindles in the iliocostalis muscle. In the mid-thoracic region (T5–T8), the three peaks noted were progressively lower from medial to lateral, and were due to spindles in the semispinalis, spinalis and multifidus muscles medially, the longissimus muscle in the intermediate position, and the iliocostalis muscle laterally.

In the lower thoracic region (T9–T12), the peak observed was due to an increased number of spindles in the longissimus muscle.

The peaks of spindle distribution in the lumbar region were higher than those of the thoracic whilst the sacral region showed the lowest maxima.

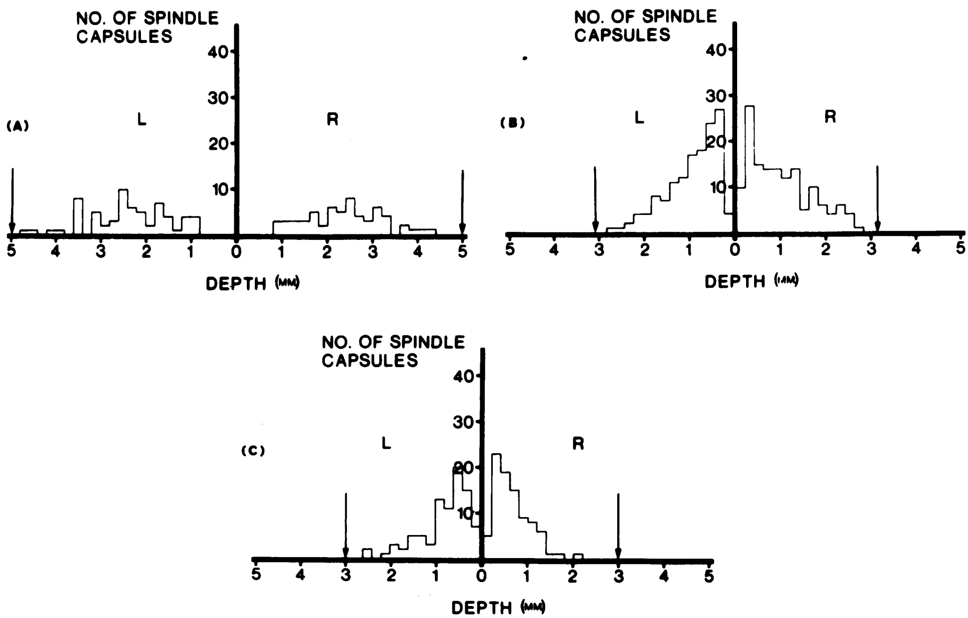

Fig. 5. Histograms showing the depth of spindle distribution in the cervical region. The muscles of this region were grouped and studied as follows: (A) spinalis and multifidus muscles; (B) semispinalis capitis and cervicis muscles; (C) longissimus capitis and cervicis muscles. Arrows indicate the maximum depths of the muscles.

Depth of spindles from the dorsal surface of the postvertebral muscles

This reflects the distribution of spindles in the coronal plane from the thoracolumbar fascia. The spread of spindles and depth of peaks of spindle distribution from the thoracolumbar fascia are illustrated in Figures 5 and 6 and in Tables 4, 5 and 6.

Cervical region

In the semispinalis muscles, there were fewer spindles in the deep parts of the muscles, most spindles being located in the superficial half of the muscle, with a peak at a depth of 0·2–0·4 mm from the thoracolumbar fascia. The peaks in the spinalis muscles and in the multifidus muscle were located in their cores. In the longissimus capitis and cervicis muscles, more than half the spindles found were located in the superficial half, with a peak at 0·4 mm from the surface.

Thoracic region

In the semispinalis thoracis and spinalis thoracis muscles, spindles were concentrated in their cores. The highest concentration of spindles in the multifidus muscle was recorded in the mid-thoracic region. The longissimus muscle showed a more uniform pattern of distribution of its spindles in the thoracic region. The depth at which spindles were located increased from upper to lower thoracic regions, but generally the majority of spindles were located in the superficial parts of the muscle. Spindles in the iliocostalis muscle were noted as mainly in the medial half. Peak distribution in upper, mid- and lower thoracic regions was found to be in the core of the muscle.

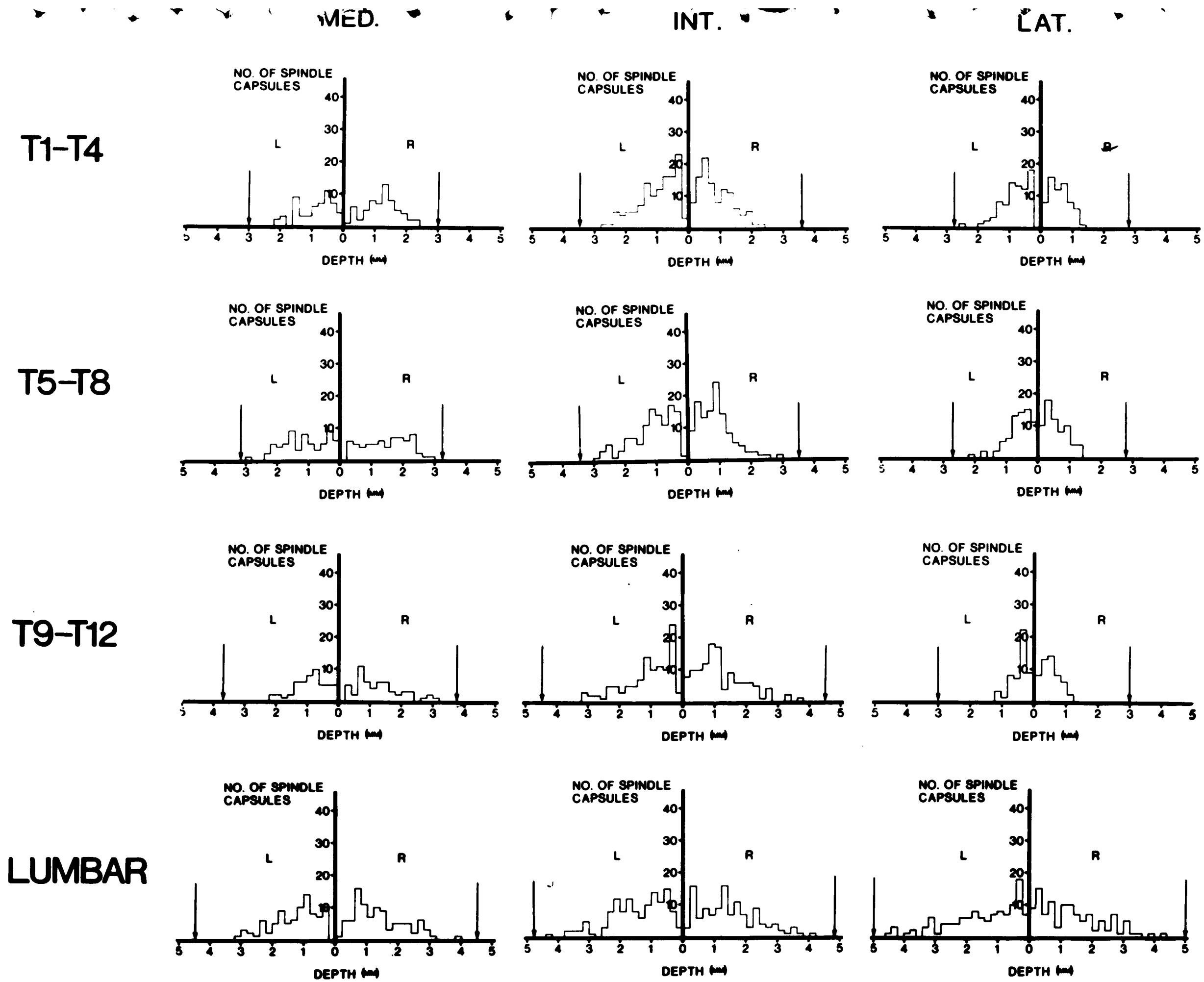

Fig. 6. Histograms showing the depth of spindle distribution in the thoracic and lumbar regions. In these regions, depth of spindles in the medial (MED), intermediate (INT) and lateral (LAT) columns were measured in the upper (T1–T4), mid- (T5–T8), lower (T9–T12) thoracic regions and the lumbar region. Arrows indicate the maximum depths of the muscles.

Lumbar region

Although spindles were found in the entire depth of the erector spinae muscle, peak distribution in its medial, intermediate and lateral parts was superficially located, at depths of 0·6–0·8 mm from the thoracolumbar fascia.

Sacral region

The distribution of spindles within the conjoint mass of the longissimus, iliocostalis and multifidus muscles was even and showed no clear-cut preponderance in any part.

DISCUSSION

The close apposition of the postvertebral muscles to the vertebral column, whose structure and mobility varies markedly in the different regions, poses special problems. In the erect posture, the tendency of the column to buckle is prevented by the strong ligaments associated with the joints, with negligible postvertebral muscle activity (Floyd & Silver, 1955; Portnoy & Morin, 1956; Joseph & McColl, 1961; Morris, Lucas & Bresler, 1961; Waters & Morris, 1972; Andersson, Ortengren & Herberts, 1977). The differing positions of the body's line of weight lead to variable demands on the different segments of the postvertebral muscles during different postures and movements. Intrinsic movements of the vertebral column occur primarily in the cervical and lumbar regions, whilst the thoracic region allows some axial rotation but minimal flexion and extension because of splinting by the rib cage. The region of functional transition between the thoracic and lumbar regions is commonly marked by a zygapophyseal joint comparable with a carpenter's mortice. The transition is usually seen between T12 and L1 but may sometimes occur between T11 and T12 or even T10 and T11 (Davis, 1956*a*, *b*). If present, this joint does not allow any rotational movement (Davis, 1956*a*). The functional coordination of the different segments of this multi-jointed system is clearly of interest. Etemadi (1963, 1974) estimated the number of slips in each column of the group; but there appears to be no information on the pattern of functional overlap of the slips. Nevertheless, the contribution of individual slips to any observed movement of the vertebral column is thought to be intricately integrated with the contraction of neighbouring slips. This means that there is probably a pattern of recruitment of slips depending on the nature of the movement to be performed. This would depend on afferent input into the central nervous system from these muscles. Gregor (1904) suggested in his report that there was a relationship between his figures of muscle spindle density within these muscles and their reported physiological activity, although he conceded that the relationship was not a simple one; but he did not make any functional studies himself and he did not study all parts of the intrinsic postvertebral muscles. The present study extends the morphological findings of Gregor and shows that all levels and units of the group are supplied with muscle spindles.

The spindle contents of the medial, intermediate and lateral columns in the present study, expressed as percentages of the total spindle count, are 37·1 %, 45·4 % and 17·5 %, respectively, on the left side, and 37 %, 44·5 % and 18·5 %, respectively, on the right side. The corresponding figures from Gregor's (1904) report are 20 %, 45·1 % and 34·9 %. The present figures match those of Gregor for the intermediate column, whilst those for medial and lateral columns appear to be reversed. The muscles in the present study were not dissected out, and therefore their normal relationship with skeletal elements could be used in identifying them. Reversal of figures for medial and lateral columns can thus be ruled out. In Gregor's extensive study, the possibility that individual muscles were dissected out cannot be excluded. The chance that figures for the muscles may have been reversed therefore exists, although the meticulous nature of the study makes this unlikely. Another possible explanation for the discrepancy lies in the fact that Gregor's graphs were incomplete; it is possible that the actual percentages for the entire columns of muscles would be different from what has been deduced from the graphs.

Distribution

The distribution of spindles in the cervical muscles has been noted, in the present study, to be mainly in the superficial parts of each muscle; in these positions they were seen to be arranged in well defined zones of high spindle concentration. In human suboccipital muscles, Cooper (1966) observed that the spindles lay almost in a straight line on the long axis of the muscles, inside an inner oval. Spindles in those muscles were rarely situated within 0·75 mm of the superficial or deep surfaces of the muscles. Clearly, the location of muscle spindles in the suboccipital muscles differs from that in the cervical part of the extensor muscle mass, although, in both cases, spindles were noted to be distributed in well defined zones corresponding to the positions of the major intramuscular nerve trunks. This finding agrees with the earlier reports of Gregor (1904), Barker & Chin (1960), Barker & Ip (1961), Barker (1962, 1974), Chin, Cope & Pang (1962) and Cooper (1966). In the thoracic, lumbar and sacral regions of the postvertebral muscles, the predominance of muscle spindles in the deeper parts of the muscle was also found to be consistent with the distribution of the major intramuscular nerve trunks.

SUMMARY

Serial transverse sections of intrinsic postvertebral muscles of a 21 weeks old human fetus were studied after staining with haematoxylin and eosin, Van Gieson's stain with Weigert's haematoxylin, and Glees' silver impregnation technique.

Muscle spindles have been demonstrated throughout the entire length of the intrinsic postvertebral muscles. The total numbers of spindles on the right and left sides were determined. Using a special technique of graphic reconstruction, the locations of spindles within these muscles were plotted. Regional differences in the numbers and distribution of spindles were noted. The significance of these findings has been discussed.

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