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A study of motoneuron groups and motor columns of the human spinal cord

R. V. ROUTAL AND G. P. PAL

Department of Anatomy, M P Shah Medical College, Jamnagar 361 008, *Gujarat, India*

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ABSTRACT

Eight normal human spinal cords were studied for motoneuron (Mn) groups and columns. Spinal segments (C1 to Coc.) were identified and embedded in paraffin wax. Serial cross sections were cut at 25 μm and stained by cresyl violet. Cross-sectional profiles of the spinal cord were traced for each segmental level and the outlines of the various Mn groups superimposed. These charts (maps) were used to examine intra and intersegmental changes in the relative positions of the columns. An attempt was made to provide topographical picture of Mn groups of individual segments. In the cervical region neuronal groups were more numerous but smaller and less distinct, while in the lumbosacral region they were fewer, larger and at many levels better circumscribed. The average number of Mn groups at any segmental level was 3–4 and never exceeded 5. C4, C5, C6, C7, L4, L5 and S1 contained numerous Mn groups. Maximum intrasegmental changes were noted at C3, C4, C7, T1, and S2, while at C5, C6, all thoracic, L1 L2 and L3, the pattern was constant throughout the segment. Eleven motor columns were traced in the human spinal cord. Column 1 belonged to the medial division and columns 2–11 to the lateral division of the ventral grey horn. Columns 1 and 2 were the most extensive as they were traceable from the lower medulla to S3 segment. Columns 3–8 were confined to cervical segments (including T1), while columns 9–11 were traced in lumbosacral segments. In general, motor columns followed a definite mode for their appearance and disappearance. Many of them showed rotation from a dorsal to a ventromedial direction.

Key words: Spinal motoneurons.

INTRODUCTION

Many attempts have been made to study the distribution of motoneurons (Mns) in the human spinal cord. Bruce (1901), Dejerine (1902), Jacobsohn (1908) and Massazza (1922, 1923, 1924) studied the spinal cord almost completely, where as Onuf (1890), Sano (1904) and Van Gehuchten & De Neef (1900) studied only the lumbosacral enlargement. Elliott (1942) attempted to investigate motor columns in the cervical and lumbosacral enlargements, while Romanes (1941) investigated Mn groups in same area of fetal cord. Sharrard (1955) made an attempt to study motor columns in poliomyelitis patients. Reports on the localisation of isolated nuclei such as the phrenic (Collins, 1894; Sano, 1898; Kristenson, 1934; Keswani & Hollinshead, 1956), the spinal nucleus of the accessory nerve (Pearson, 1938) and Onuf's nucleus (Schroder, 1981; Pullen et al. 1997) are also available.

Figure 1 includes a diagrammatic representation of all previous major findings reported by Elliott (1942). It is evident that findings were different with regard to the total number of columns and their subdivisions, the location of columns and their interrelations and their segmental extent. Hence it is very difficult to decide which pattern should be considered as standard. Elliott (1942) suggested that lack of sufficient material, standardised technique and confusing nomenclature were responsible for the chaos. He also pointed out that findings of many of the previous investigators, who are widely quoted (Bruce, Jacobsohn, Massazza and Van Gehuchten) were based on a single spinal cord.

Elliott (1942) evolved a method to trace Mn groups and columns which has been widely accepted. He

Correspondence to Dr R. V. Routal, C -18 Medical Campus, Jamnagar 361 008, Gujarat, India

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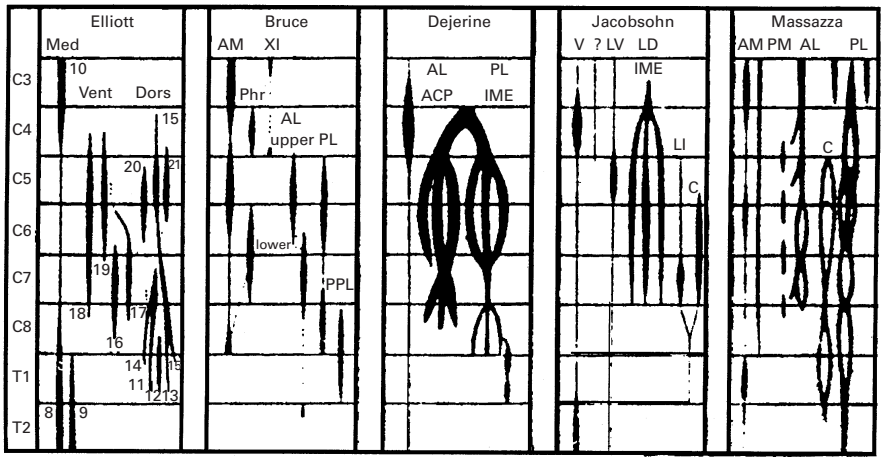

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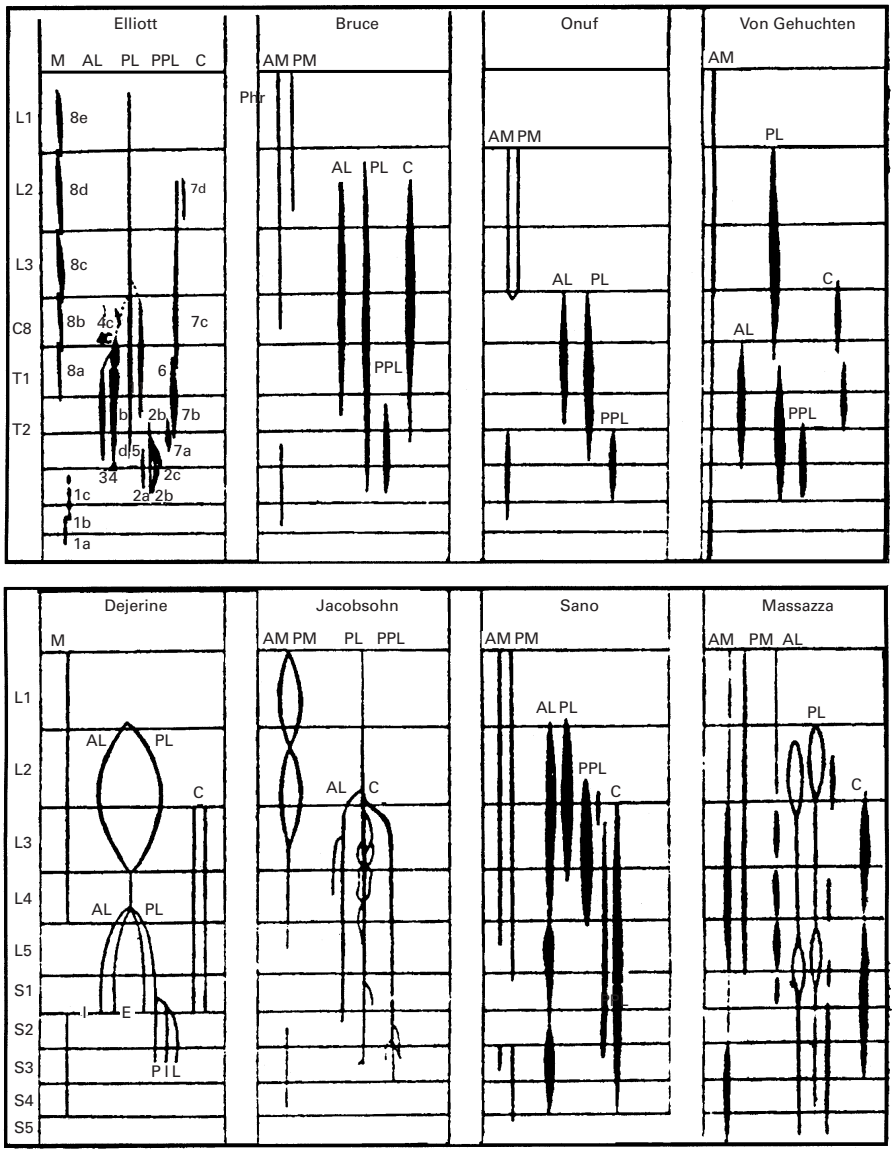

Fig. 1. For legend see opposite.

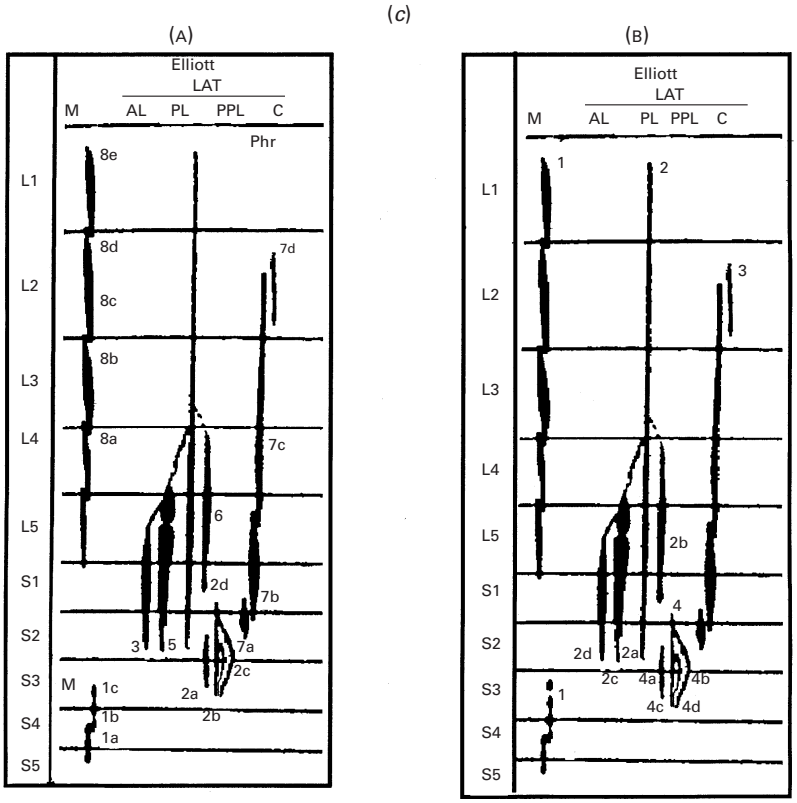

Fig. 1. Diagrammatic representation of findings of previous investigators. (*a*, *b*) motor columns of lumbosacral and cervical enlargements respectively (from figs. 1–3, Elliot (1942). (C) Comparison of numbering method of Elliott and the present study. (A) Motor columns numbered according to Elliott (1942). (B) Elliott's columns numbered according to the present study.

designated the columns by a numbering method, to avoid the confusion created by previous nomenclatures. Despite his efforts, he was unable to provide a perfect technique for tracing motor columns. Nevertheless, as mentioned below, it was found that his method has few major errors. He proceeded from the caudal end of the spinal cord (i.e. S3), where the columns terminate, and hence it became very difficult to differentiate between the main column and its subdivisions. Therefore subdivisions might be regarded as separate columns and more columns than the actual number might be traced. This led to misinterpretation of the actual pattern of columns (Fig. 1 *c*). Secondly, he traced motor columns in the cervical region omitting most of the thoracic segments. Thus continuity of certain columns linking the lumbosacral and the cervical regions was lost. Moreover, cervical columns were numbered in continuity with lumbosacral columns which further enhanced the confusion.

While tracing motor columns of the spinal cord, it should be remembered that, despite its segmental pattern, the spinal cord is a continuous column of white and grey matter. Hence it becomes more logical that columns should be traced from the level of their commencement, instead of tracing them in the cervical and lumbosacral enlargements. To obtain a correct pattern of columns the complete spinal cord should be traced in a craniocaudal direction, as the columns show a branching pattern in same direction (Fig. 1). For correct identification of columns and their successive subdivisions it is essential that columns should be numbered according to their appearance in a craniocaudal direction, which simplifies the pattern.

As experimental studies are out of question in the human spinal cord, there is scope for clinical and developmental studies which require a sound anatomical basis. The present investigation was undertaken to provide a platform for such studies. Motor columns were traced with improved methodology, to define the pattern of motor columns of the complete human spinal cord. An attempt was also made to provide details of Mn groups of individual segments, including intrasegmental changes.

MATERIALS AND METHODS

The material consisted of 8 human spinal cords collected from normal male bodies, donated to the Medical College for the purpose of dissection with an

age range of 28–60 y. Segments were identified with the help of spinal nerves. In each segment, sides (right, left) and ends (cranial, caudal) were distinguished by nick marks. Segments were embedded routinely in paraffin wax. Serial cross sections were cut at 25 μm and stained with cresyl violet.

Mn groups and columns were traced by Elliott's (1942) method. With the help of a microprojector, images of cross sections were projected at a constant magnification. In the first section the periphery of the ventral horn was drawn, within which Mn groups were demarcated by their outlines. Similarly Mn groups of the succeeding 19 sections were superimposed by adjusting the outline of their ventral horn with that of the first section. Thus each chart represented details of 20 serial sections, i.e. 0.5 mm thickness of tissue. Groups were identified with the help of charts because in individual sections it was difficult to differentiate a genuine group and a local cluster of neurons. On tracing them in successive sections, local clusters did not appear after a few sections, while neurons belonging to a group persisted. Each segment was represented by a set of charts. Groups were traced from serially arranged charts and within a segment, changes in pattern of groups were noted. As the charts are the summation of 20 serial sections they cannot be compared with a single cross section. It may happen that a single cross section may not provide all the details as depicted in a chart, the reason being that all groups are not always well marked in a single section because of a chance distribution of neurons.

Motor columns were reconstructed from cross sections. Columns were designated by numbers. These numbers differed from those of Elliott (1942). Columns were numbered in order from medial to lateral. Column 1 was allotted to the most medial column at C1 segment, succeeding numbers were allotted to the columns of lateral division in order of their appearance in craniocaudal direction.

RESULTS

The observations are divided into 2 parts. The first deals with a description of Mn groups in cross sections, and the second provides an account of the motor columns.

Motoneuron groups

It is a well accepted fact that in the spinal cord, motoneurons are organised into medial and lateral divisions. The medial division consist of a single group while the lateral division is made up of many groups, their number differing in the cervical, thoracic and lumbosacral regions.

In the present study a total of 11 groups was observed throughout the spinal cord. Group 1 represented the medial division, group 2 and subsequent groups were the members of the lateral division. Groups 1 and 2 were observed throughout the spinal cord, while groups 3–8 and 9–11 were confined to the cervical (including T1) and lumbosacral regions respectively.

Figures 2–11 should be constantly referred to for following observations. Mn groups were observed from C1 to S3 prominently and constantly but below S3 segment there were only few scattered motoneurons in the ventral horn. At the level of C1, 2 groups were observed in the grey matter. The medially situated group 1 was divided into subgroups 1a (ventral) and 1b (dorsal). Group 2 was dorsolateral to 1a, occupying the central area of the ventral horn (Fig. 2). To confirm whether these 2 groups were derived from a common pool, sections of the lower medulla, below the pyramidal decussation were also studied. It was found that groups 1 and 2 were 2 separate entities (Fig. 2). Subgroup 1c was a new addition to group 1 at the end of C2, and was more prominent at C3 (Fig. 3). It merged with 1a and 1b at C4 and C5 and was not traceable below C5. Thus in the remaining cervical segments together with T1, group 1 was represented by 1a and 1b (Figs 2–7). In the lateral division groups 3, 4 and 5 appeared at C2, C3 and C4 respectively. Therefore from C2 to C4, Mn groups consistently increased in number and accordingly intrasegmental changes were noted at C3 and C4, (Figs 3, 4). Groups 2, 4 and 5 were observed with 2 subgroups, however 2a persisted for a short distance and disappeared at C3 (Fig. 3), where as 2b persisted up to mid C5. From caudal C4 to C5, subgroup 2b was an ill defined group. Hence at caudal C4, groups 1, 3, 4 and 5 were the prominent groups and with minute changes, these groups were consistently observed at C5 and C6 (Fig. 4). Subsequently groups 3, 4 and 5 disappeared in the upper two thirds of C7. At the same time group 6 appeared at the cranial end of this segment, increased in size and divided into 3 subgroups occupying a large area of the ventral horn (Fig. 5). Groups 7 and 8 appeared at C8 while along with them group 2 reappeared at this level (Fig. 6). Groups 6, 7 and 8 continued up to the upper two thirds of T1, hence the lower third of this segment comprised only of 2 groups, i.e. groups 1 and 2 (Fig. 7). Thus at the end of the cervical region the pattern of groups was same as

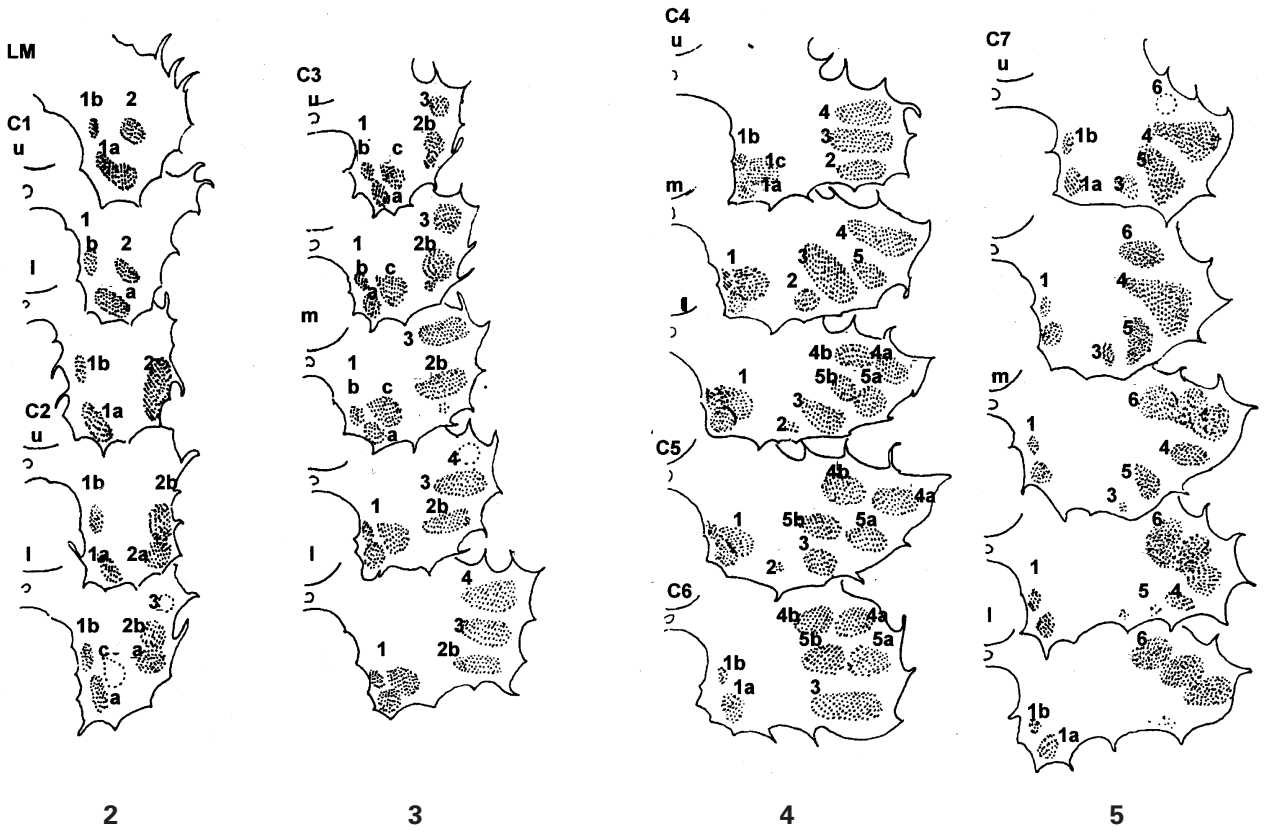

Fig. 2. Pattern of Mn groups at lower medulla (LM), C1 and C2. Stippled line depicts appearance of group or subgroup. Numbers and letters within figure indicate group and subgroups. l, lower; u, upper.

Fig. 3. Intrasegmental changes in the pattern of Mn groups at C3. Disappearance of group or subgroups are depicted by few dots. l, lower,; m, middle; u upper.

Fig. 4. Pattern of Mn groups at C4, C5 and C6.

Fig. 5. Intrasegmental changes in the pattern of Mn groups at C7.

that noted at C1. The same pattern continued in thoracic region. In the thoracic region, however, groups 1 and 2 were not always distinct; they overlapped frequently and together they appeared as a single mass of neurons (Fig. 8).

In the lumbosacral region there was a gradual increase in the number of groups. At the level of L1, the pattern observed was same as that of the thoracic segments but groups 1 and 2 were large and well set apart. Groups 9, 10 and 11 appeared at an interval of 2 segments i.e. at L2, L4 and S1; therefore in adjacent segments, i.e. L2 and L3, L4 and L5 and S1 and the cranial two thirds of S2, the pattern of groups was almost same (Figs 9–11). Group 1 disappeared at the caudal end of L4 but reappeared at S2. Group 2 was very prominent at the upper 3 lumbar segments, especially at L2 and L3, where it comprised 2 large distinct subgroups (2a, 2b) (Fig. 9). Similarly group 10 was especially prominent at L4 and L5 segments, where it divided into 2 subgroups, 10a and 10b. Each subgroup was further divided into ventral and dorsal parts. Thus group 10 was the largest group of the spinal cord at L4 and L5 (Figs 9, 10). Unlike the cervical region, all groups, i.e. groups 1, 2, 9, 10 and 11 disappeared abruptly between caudal S2 and S3 segments. Caudal to S3, the spinal cord comprised of few scattered motoneurons in the ventral horn (Fig. 11). Mn groups of the lumbosacral region were much larger and well defined. Group 2 at L1 and L2, subgroup 2a at S2, S3, group 9 at L2, L3, and subgroup 11b at S2, S3 were all well circumscribed with a definite border of myelinated fibres. They were also characterised by circular or oval shape, and traversed by vertical fibres. However, at the junction of L4/L5 and at S2, groups were not well demarcated, as the margins of the adjacent groups frequently merged with each other.

On average there were 3–4 Mn groups at each segmental level. At the level of C4, C5, C6, C7, L4, L5 and S1, the lateral division comprised more groups and subgroups, hence they were the most crowded segments of the spinal cord. At these segments Mn

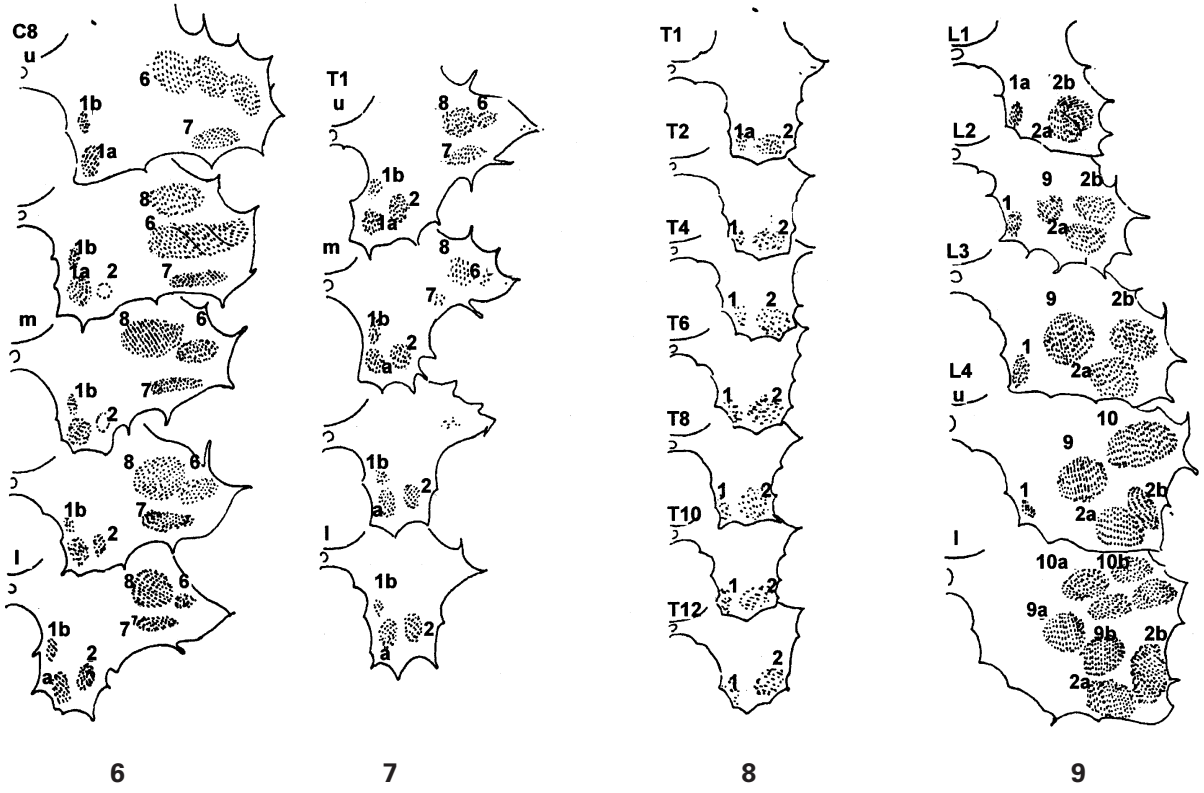

Fig. 6. Intrasegmental changes in the pattern of Mn groups at C8.

Fig. 7. Intrasegmental changes in the pattern of Mn groups at T1.

Fig. 8. Pattern of Mn groups at different thoracic segments.

Fig. 9. Pattern of Mn groups at L1, L2, L3 and L4.

groups and subgroups occupied a large area of the ventral horn. C3, C4, C7, T1 and S2 were the segments where maximum intrasegmental changes (i.e. change in number, size and position of Mn groups) were noted, while at C5, C6, all thoracic segments (except T1), L1, L2 and L3, pattern was constant throughout the segment.

Motor columns

Eleven motor columns were traced within the spinal cord. Column 1 represented the medial division and corresponded to the medial column of previous reports (Onuf, 1900; Bruce, 1901; Dejerine, 1902; Jacobsohn, 1908; Massazza, 1922–23–24; Elliott, 1942). The remaining 10 columns belonged to the lateral division.

Column 1 (Figs 12, 13, 16)

Column 1, the most extensive column of the spinal cord, extended from the lower medulla to S3 segment, with a short discontinuity between caudal L4 and S1. Throughout its course column 1 was situated very close to the medial margin of the ventral horn. In the cervical region it comprised 1a (ventral), 1b (dorsal) and 1c (lateral) subdivisions. Though columns 1a and 1b were present throughout the cervical region, subgroup 1b was ill defined and became reduced in size especially caudal to C4. Subdivision 1c was confined to C3–C5 segments only, but was more prominent and discrete at C3 segment, where it was made up of large densely packed neurons. Below C3 it merged with 1a and 1b, bridging the gap between them. Because of 1c, column 1 was thickest and prominent at C3–C5 (Fig. 12). In the thoracic and the lumbosacral regions column 1 was represented by subdivision 1a. Hence in those regions it was slender as compared with column 2. In the thoracic region, except at its cranial and caudal segments, 1a was comprised of small, loosely packed neurons (Fig. 13). In the lumbar region it was a well defined column. At the lumbosacral junction, 1a was interrupted and with regard to the level of interruption few variations were noted. On average, it was interrupted between caudal L4 and the cranial one third of S2. The sacral part of the column was very short and slender, made up of smaller neurons (Fig. 16).

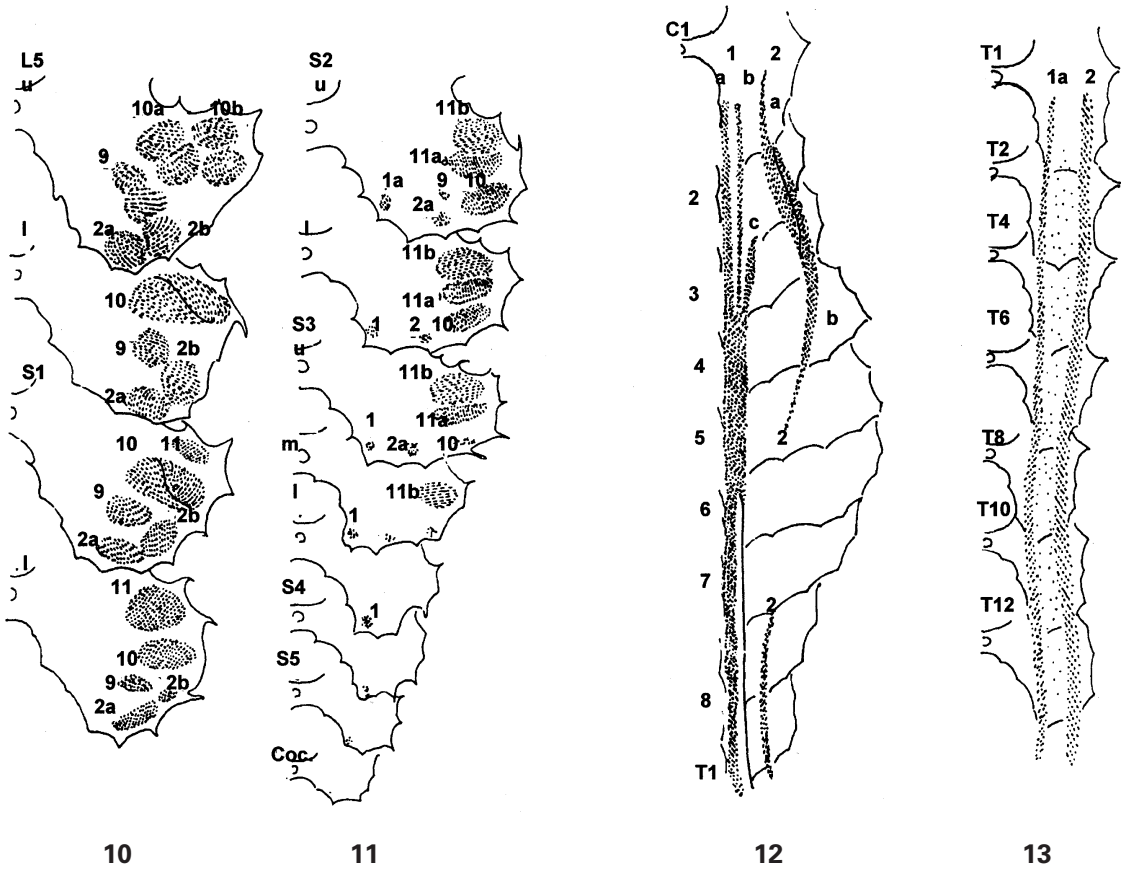

Fig. 10. Pattern of Mn groups at L5 and S1.

Fig. 11. Pattern of Mn groups at S2, S3, S4, S5 and coccygeal (coc.) segments.

Fig. 12. Motor columns 1 and 2 in the cervical region, their position in the ventral horn at different segmental levels and their main divisions.

Fig. 13. Motor columns 1 and 2 in thoracic region.

Column 2 (Figs 12, 13, 16)

Column 2 was another long spinal cord column and longest of the lateral division, running lateral and parallel to column 1. It also extended from the lower medulla to S3, but discontinued at C6 and C7. Because of this discontinuity column 2 was divided into the upper cervical and the lower thoraco-lumbosacral part. The cervical part was well defined up to C4 but continued in C5 as a rudimentary extension. At the cranial end column 2 was situated centrally, dorsal to 1a, but shifted laterally in its middle part (Fig. 2). At its terminal end, column 2 again obtained a central position. Thus it was a curved in craniocaudal direction. At C2 it divided into 2a (ventromedial) and 2b (dorsolateral) subdivisions. 2a was the shorter, terminating at C3, while 2b continued to C5 (Fig. 12).

In the thoracic region (Fig. 13) column 2 was slender and undivided consisting of small loosely packed neurons. It was situated very close to column 1. In the lumbar region column 2 shifted laterally and was confined to the ventrolateral end of the grey matter, Except at the upper third of L4, it was divided into 2a (ventromedial) and 2b (dorsolateral) subdivisions. They were more prominent and distinct at L2 and L3, hence column 2 was thickest at those segments (Figs 6, 9). It tapered towards its caudal part as subdivision 2b terminated at the caudal end of S1 (Fig. 10). Subdivision 2a, however, continued to S3 as a slender terminal part comprised of small neurons traversed by vertically running fibres and surrounded by a well defined border of circular fibres. Within S2 subdivision 2a shifted more ventrally and medially (Figs 11, 16). Throughout its course column 2 maintained a constant relation with column 1 which was situated medial to it. Dorsolaterally column 2 was related with column 3 in the cervical region (Figs 3, 4). In the lumbosacral region column 9 was dorsomedial to column 2 (Figs 9, 10). Topographically column 2 corresponded to the anterolateral column of previous reports.

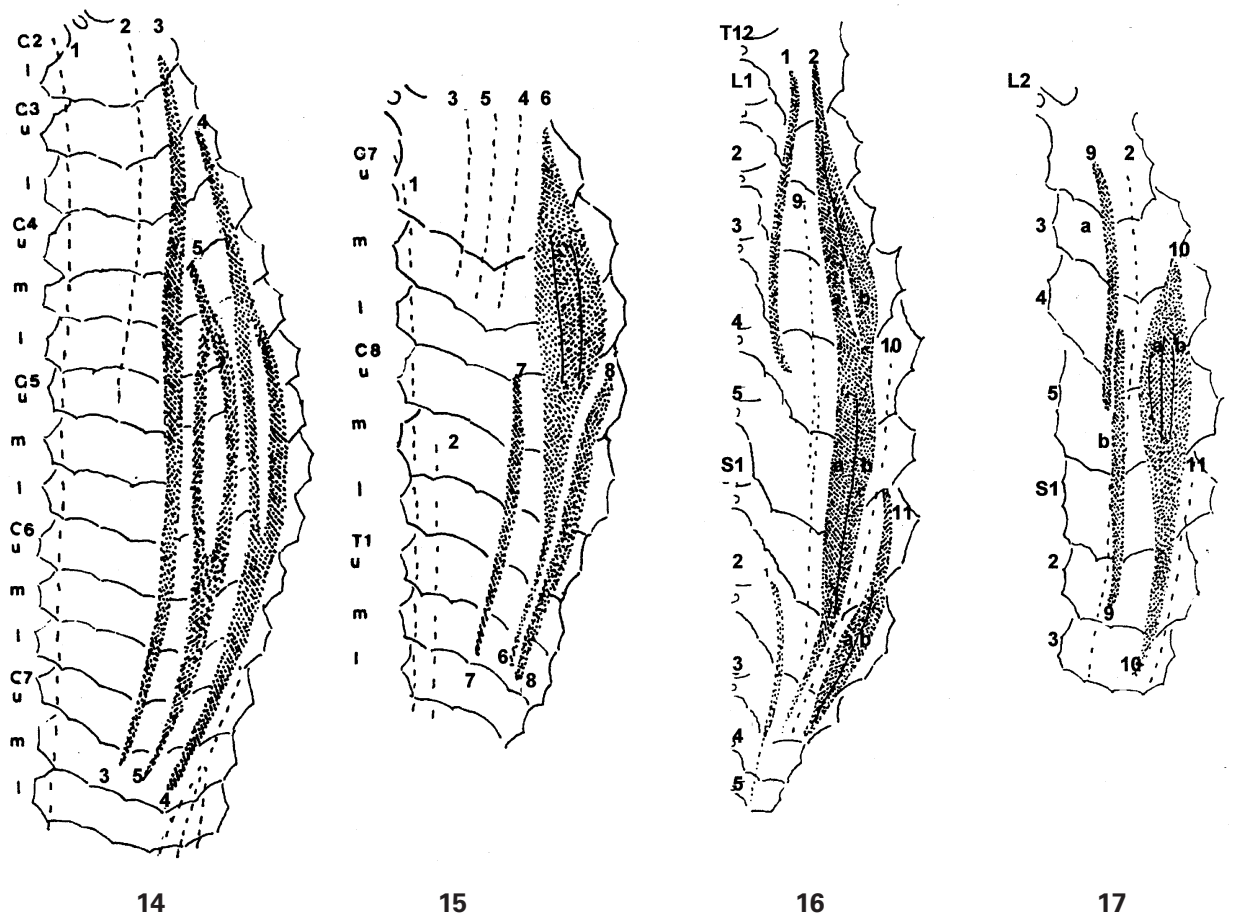

Fig. 14. Extension of motor columns 3, 4 and 5, their position in the ventral horn at different segmental levels and their main divisions. For reference, columns 1, 2 and 6 are shown as stippled lines.

Fig. 15. Extension of motor columns 6, 7 and 8, their position in the ventral horn at different segmental levels and their main divisions. For reference, columns 1, 2, 3, 4 and 5 are shown as stippled lines.

Fig. 16. Motor columns 1, 2, and 11 in the lumbosacral region showing their postion in the ventral horn and their main divisions. For reference, columns 9 and 10 are shown as stippled lines.

Fig. 17. Extension of motor columns 9 and 10, their postion in the ventral horn and their main divisions. For reference, columns 2 and 11 are shown as stippled lines.

Column 3 (Fig. 14)

Column 3 was a long cervical column. Its cranial end was located at the junction of C2 and C3 segments (Figs 2, 3). Caudally, it extended to the cranial third of C7. Initially column 3 was situated between columns 2 and 4, but it assumed a medial position due to the discontinuity of column 2 at C6 and C7 segments. In those segments column 5 was dorsal to column 3. At its termination column 3 shifted more medially and very close to the ventral border of the grey matter (Fig. 5).

Column 4 (Fig. 14)

As column 4 was located dorsolaterally throughout its extent, i.e. C3–C7, it can be considered as a dorsolateral column according to previous nomenclature. At the caudal third of C4 column 4 divided into 2 subdivisions, 4a (ventrolateral) and 4b (dorsomedial) (Fig. 4). These subdivisions were quite distinct and thickest at C4 and C5 but at C6, 4a and 4b fused to form a single wide column which tapered towards its terminal end, where it shifted ventrally close to the ventral border of the grey matter (Fig. 5).

Column 5 (Fig. 14)

Unlike other columns, column 5 appeared between 2 pre-existing columns, i.e. column 3 and 4, at the level of C4 (Fig. 4). It descended to the level of C7. In its initial course column 5 was divided into 5a (ventrolateral) and 5b (dorsomedial) subdivisions, lying ventral and parallel to the 2 subdivisions of column 4. The subdivisions 5a and 5b were very distinct and

prominent at C5 but started merging at C6 to form a single column. Column 5 gradually tapered towards its terminal end and like column 3 it also shifted ventromedially.

Column 6 (Fig. 15)

Column 6 was one of the shortest of the cervical region, extending between C7 and T1. Within C7, it split into 3 distinct subdivisions, and together they occupied a large dorsolateral area of the ventral horn (Fig. 5). At C8 column 6 was again single. As column 8 increased in size column 6 shifted laterally and retained the same position until its termination.

Column 7 (Fig. 15)

Column 7 was short and slender, running between C8 and T1. Unlike other columns it appeared ventral to a pre-existing column, i.e. column 6 and was close to the ventral border of the ventral horn (Fig. 6). Column 7 maintained same position throughout its extent.

Column 8 (Fig. 15)

Column 8 was the last to appear in the cervical region. It appeared dorsal to column 6 at C8 and maintained proximity with that column until its termination. Columns 6 and 8 were the typical short posterolateral columns mentioned by previous investigators.

Column 9 (Fig. 17)

Column 9 commenced at L2 segment dorsal to column 2. In the lumbar segments its position resembled the central column of previous reports. Caudally, column 9 shifted a little laterally and terminated at the caudal end of S2. It was divided into 9a (L2 to L5) and 9b (L4 to S2) subdivisions, and both overlapped each other at L4/5 junction. Columns 2 and 10 maintained a constant relationship at the ventral and dorsolateral aspects of column 9 respectively (Figs 9, 10).

Column 10 (Fig. 17)

Column 10 was a dorsolateral column extending between L4 and S3. Soon after its commencement it split into 2 divisions, 10a (medial) and 10b (lateral). Each further divided into ventral and dorsal subdivisions (Figs 9, 10). They were prominent and distinct subdivisions, comprised of large motoneurons at L4 and L5. Thus column 10 was the thickest at those segments. At the caudal end of L5 all divisions fused to form a single large column, which gradually tapered towards its terminal end. At its termination column 10 shifted more ventrally at the junction of the grey and white matter.

Column 11 (Fig. 16)

Column 11 was the shortest column observed in upper sacral segments, i.e. S1–S3. It appeared dorsal to column 10. At the level of S2, column 11 divided into 11a (ventral) and 11b (dorsal) subdivisions (Fig. 11). Although both divisions were situated very close together, 11b was distinguished by a well defined outline. It was a typical post-posterolateral short column of the lumbosacral region.

DISCUSSION

To define Mn groups in the spinal cord is a difficult and tedious task. The reason is the Mn groups do not have any definite natural boundary and neither their size nor their shape is constant. A random distribution with respect to the morphological form of motoneurons is another factor for variation. Similarly within a cross section, bilateral differences in their morphology are very common. However, such errors can be corrected by adopting Elliott's technique, where Mn groups are demarcated with the help of charts. Each chart represents details of 20 serial sections which is equal to 0.5 mm tissue depth. When comparing individual motor columns in different spinal cords, variations in their vertical extent were common. Their vertical extent varied within a limit of one or one and half segments. It is quite possible that the difference in vertical extent of columns might be due to a prefixed or postfixed pattern of the limb girdle plexuses. Despite these differences, a basic pattern of motor columns with regard to their total number and major subdivisions, their position and interrelations, and their mode of apprearance and disappearance, was very constant in all specimens.

The motor columns of the human spinal cord have been studied by several investigators. Despite many attempts one fact that has emerged is that there is general disagreement. Figure 1*a*, *b* reveals the same fact. Most previous studies were confined to the cervical and lumbosacral enlargements. The only common finding of previous reports was that motor columns were classified into medial and lateral divisions.

For the medial division, in the cervical enlargement,

except for Massazza no one has mentioned subdivisions. In the present study in the cervical region column 1 was represented by 3 subdivisions, i.e. 1a, 1b and 1c (Figs 1*b*, 18). In the lumbosacral enlargement, except for Dejerine, Elliott and Van Gehuchten all have reported anteromedial and posteromedial subdivisions in the medial division. In the present study subdivision 1a represented the medial division and it was interrupted at L4–S1. Except for Massazza and Van Gehuchten & De Neef, all previous studies have reported such an interuption, but segmental level variations were observed (Figs 1*a*, 18).

For the pattern of motor columns of the lateral division, the findings are chaotic. In the cervical enlargement the findings of the present study did not show similarities with any previous report. However, the postposterolateral column of Bruce, columns 11, 12 and 14 of Elliott and columns 6, 7 and 8 of the present study were typical short posterior columns observed in caudal segments of the cervical enlargement (Figs 1*b*, 18). In the lumbosacral enlargement columns of the lateral division of the present study showed little resemblance with that of Bruce (Figs 1*a*, 18).

As mentioned earlier, inadequate material and lack of standard technique were the major reasons for all discrepancies. We further emphasise that with a few corrections to Elliott's technique, i.e. tracing columns craniocaudally and with continuity of the spinal cord, a more correct and clear pattern of motor columns can be obtained.

Figure 8 reveals that the thoracic segments comprised a minimum number of groups (T1 is always considered together with the cervical region, as certain cervical columns extended into this segment). Groups 1 and 2 of this region were not as distinct as they were in other regions. The laminar pattern of the spinal cord, as suggested by Rexed (1952) is different in the thoracic region as compared with the cervical and lumbar regions. Here Rexed laminae VII, VIII and IX are arranged in order from dorsal to ventral, hence lamina IX is confined to the ventral tip of the grey matter. Groups 1 and 2 were lodged in this narrow area. It was observed that whenever both groups were comprised of a large number of neurons their margins were obliterated. Hence frequently, they appeared together as a single mass. Thus the thoracic region comprised columns 1 and 2, situated very close together (Fig. 13).

A similar pattern was observed at C1 and L1 but both groups were quite distinct (Figs 2, 9). Thus at the beginning of the cervical region columns 1 and 2 were observed in the ventral horn (as both descended from the level of the lower medulla). Figure 18 depicts segmental levels of columns of the spinal cord. In the upper cervical region a set of 3 columns, i.e. columns 3, 4 and 5 appeared between lower C2 and C4 . These columns descended to C7. Another set of 3 columns, i.e. columns 6, 7 and 8 appeared between C7 and C8 and terminated at the upper two thirds of T1. Therefore the caudal end of T1 consisted only of columns 1 and 2; at the end of the cervical region the pattern of columns was thus same as observed at its cranial end (i.e. C1). Since columns 3 to 8 were confined to the cervical region they can be designated as cervical columns. According to their extent these can be further classified as long (columns 3–5) and short (columns 6–8) cervical columns. Thus the maximum number of columns was observed in the cervical region.

Similarly at the beginning of the lumbosacral region, i.e. L1, the same 2 columns (i.e. columns 1, 2) were observed. Other columns of the lateral division, 9, 10 and 11, appeared at L2, L4 and S1, respectively. Thus columns 9 and 10 were long and column 11 was a short lumbosacral column. Only 3 columns were added in the lateral division of the lumbosacral region, just half of those of the cervical region (Fig. 18).

Over all columns, 1 and 2 were the 2 long columns of the spinal cord. Almost all previous studies have reported a discontinuity of column 1 at the lumbosacral junction with little variation (Fig. 1). Similarly in the present study variations were also observed but, on an average, column 1 was discontinuous between caudal L4 and cranial third of S2. Figure 1 also shows that the majority of investigators have reported 2 subdivisions of column 1 in the cervical and the lumbosacral regions. They were referred to as ventromedial or anteromedial and dorsomedial or posteromedial subdivisions. With regard to column 1, the findings of the present study differ from previous ones. We observed 3 subdivisions, i.e. 1a, 1b and 1c in the cervical region but in rest of the spinal cord column 1 was represented only by 1a. Since all 3 subdivisions were observed only at C3–C5, column 1 showed considerable enlargement at those segmental levels (Figs 12, 18). This was due to subdivision 1c which was confined to the above mentioned level and was more prominent as compared with the other 2. Elliott (1942) mentioned such an enlargement in this column at C3 and C4 which he referred to as the phrenic nucleus (Fig. 1). Bruce (1901) reported a separate phrenic nucleus at the level of C4, lying lateral to his medial column (Fig. 1). Keswani & Hollinshead (1956) investigated a phrenic nucleus in

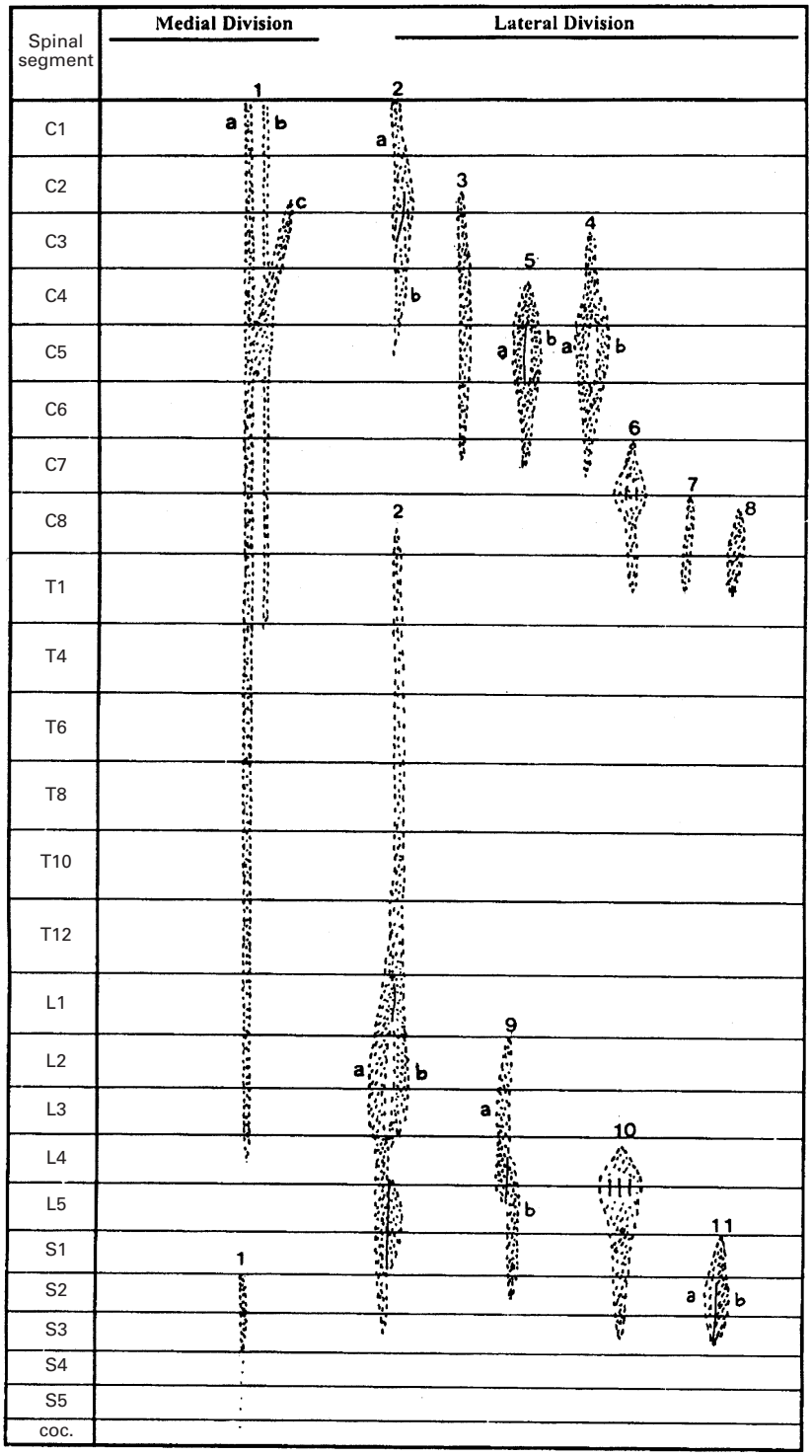

Fig. 18. Segmental extent of motor columns of complete human spinal cord. The thoracic region is represented by alternate segments to maintain the proper size of the diagram. The height of segments is shown proportionate to their actual height.

adult human spinal cord, between C3 and C5, as part of a medial column (corresponding to column 1 of the present study). His description of the human phrenic nucleus exactly tallies with the subdivision 1c of column 1. This provides strong support for the possibility of 1c being a phrenic nucleus. Almost all textbooks state that the medial column of the spinal cord innervates axial musculature, hence column 1 can be accepted as supplying axial musculature.

Another long column in the present study was the column 2. It was the longest of the lateral division. Except for Jacobsohn (1908, quoted by Larsell, 1951) no one has reported such an extensive column in the lateral division. Jacobsohn reported an anterolateral

column between C2 and S4, situated lateral to the medial column. In the cervical and lumbar regions he reported an anterior column intervening between medial and anterolateral columns. Thus his anterolateral column has less resemblance to column 2 of the present study. With respect to the morphology of column 2 it divided into 2 halves as it discontinued at C6 and C7. The upper cervical half extended from the lower medulla to C5, while the lower half was much longer and descended between C8 and S3. The thoracolumbosacral half of column 2 further can be divided into the thoracic and the lumbosacral parts on the basis of morphological differences. In the thoracic region column 2 was undivided and slender and made up of small loosely packed neurons, while in the lumbosacral region it comprised 2 subdivisions with densely packed large neurons. Column 2 was thickest at the level of L2 and L3, but at its terminal end, at the level of S2 and S3, it was again a slender column with small neurons which shifted more medially and ventrally (Fig 11). Thus the morphology of column 2 in the cervical, thoracic, lumbar and sacral regions was quite different. But, throughout its extent column 2 was situated next to column 1 with same vertical extent. It is interesting that the above mentioned morphologically different parts of column 2 show resemblances with the findings of the following reports. Pearson (1938, in the human fetus) and Augustine & White (1986, in the baboon) reported a spinal nucleus of the accessory nerve from the lower medulla to C5. Similarly Ueyama et al. (1990 in the Japanese monkey) reported this nucleus from the lower medulla to C6. Topographically the upper cervical part (lower medulla to C5) of column 2 of the present study very much resembled the spinal nucleus of the accessory nerve reported by these investigators.

Smith & Holliday (1983, in rat), Fedorko (1982, in cat), Mashiko et al. (1994, in cat) tried to locate motoneurons innervating vertebral and trunk muscles. According to them, in the thoracic spinal cord the medial column projects to vertebral muscles while the lateral column projects to trunk muscles which include intercostal and abdominal muscles. In the present study, columns 1 and 2 in the thoracic region correspond to the medial and lateral columns respectively. Henceforth, it is presumed that similar muscles are likely to be innervated correspondingly.

Sharrard (1955) attempted to locate motor columns for the lower limb muscles in the human spinal cord. He reported a long column situated just lateral to a column for erector spinae, projecting to muscles acting on the hip joint. This column extended from L1 to S2. Topographically it resembled the lumbosacral part of the column 2 of the present study. Recently Pullen et al. (1997) have described the morphology of Onuf's nucleus in man. In the present study we could not trace such a short and isolated nucleus in the sacral region, but the description of Onuf's nucleus reported by Pullen et al. was similar to the terminal part of column 2 from caudal S1–S3 (of the present study).

These observations suggest that the different morphological forms of column 2 at different regions may have some significance in that they might project to different body musculature including sternocleidomastoid, trapezius, intercostals, anterior abdominal wall muscles and muscles of the hip joint. Thus columns 1 and 2 were the twin columns extending from the lower medulla to the sacral region; hence both might innervate the extensive muscle mass from the neck to the caudal end of the trunk, including vertebral and paravertebral muscles. However, these speculations are based on the findings of different studies and there is no doubt that the thoracic pattern which included columns 1 and 2 is the basic pattern of the spinal cord. The same pattern was observed at the beginning of the cervical and lumbosacral regions. The columns added later were confined either to the cervical or lumbosacral regions. Thus columns 3–8 and 9–11 might project to the musculature of upper and lower limbs respectively.

The pattern of columns in the cervical and lumbosacral regions differed in many ways. A marked difference was observed in the number of columns and differences in the pattern of columns was reflected in the pattern of groups. The pattern in each cervical segment was different and there were many segments within which many changes were noted. It was found that within a segment the commencement of a column or the termination of existing columns, their divisions or any changes in their position can change the pattern of groups. Figure 18 depicts all these changes at C7. Column 6 appeared at the cranial end of this segment. Simultaneously columns 3, 4 and 5 tapered and shifted more ventromedially and eventually terminated in upper two thirds of the segment. Column 6 expanded rapidly and in lower third of the segment it was divided into 3 subdivisions. All these changes occurred in the same segment at different levels, and as a result of that several intrasegmental changes were noted at C7 segment (Fig. 5). Thus Figure 18 can explain why intersegmental and intrasegmental changes were common in the cervical region. In the lumbosacral region columns were few and they appeared at regular intervals. Each column appeared at an interval of 2 segments. As a result, the

pattern of adjacent segments was almost same (Figs 9–11). Moreover, all columns of this region terminated within a short segment, i.e. caudal S2–S3. Hence S3 showed several intrasegmental changes.

In the lumbosacral region groups were larger and distinct. Certain groups (2a, 9, 11b) at specific segmental levels were observed with a characteristic appearance. They were oval or circular in shape with a well defined border of circular fibres and traversed by vertical fibres. Such circumscribed groups observed only at a particular segmental level tempted us to suggest that they project to a specific target, which could be a muscle or muscle group. Experimental or clinical confirmation, however, is needed. In comparison, the cervical groups were smaller and less distinct. According to Romanes (1941*a*, *b*), the ill defined pattern of groups is due to the dedifferentiation of columns during development. During this period motor columns get broken up into different parts because neurons within a column are functionally different. Hence in adults, the pattern of columns (groups) is less distinct as compared with the pattern observed during early embryonic life. It is quite possible that during development the amount of differentiation of columns in the cervical region is greater as compared with the lumbosacral region. This is because movements of the upper limb are more complicated as compared with the lower limb, in particular those of the hand are more complex as compared with the foot. Experimental and clinical evidence has confirmed that the short posterolateral columns at the caudal segments of the cervical and the lumbosacral regions innervate hand and foot muscles respectively (Sharrard, 1955; Jenny & Inukai, 1983; Fritz et al. 1986*a*). An obvious difference in the number of short columns in the cervical and lumbosacral regions (3:1) also suggests that functional differences between the limbs might be reflected in neuronal organisation.

One interesting fact was noted regarding the commencement of the columns of the lateral division. The site of successive commencement of these columns was located dorsal or dorsolateral to the previous column. With every addition of a new column previous columns were pushed ventrally, and those which already reached the ventral border of the ventral horn were displaced medially. The ventromedial shifting was more prominent at the terminal end (compare the position of groups 3–5 in Figs 3–5). It was found that to accommodate a new column in the ventral horn and to provide more space for further expansion of newly appearing columns, the previous columns were shifted in a ventromedial direction. Thus columns 2, 3, 4, 5 and 10 at their cranial ends were situated dorsolaterally in the ventral horn but at their caudal ends they were located very close to the ventral border of the ventral horn and also shifted medially. Jenny & Inukai (1983) also reported a ventromedial shifting of columns in the spinal cord of the monkey. The short columns of the spinal cord failed to show shifting and maintained a constant position throughout their course. While tracing craniocaudally, such ventromedial shifting of columns was common in the cervical and lumbosacral regions. Hence in present study, the previous nomenclature was not adopted, as it was based on the position of columns in the ventral horn.

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