THE MOTOR CELL COLUMNS IN THE CERVICAL AND LUMBAR ENLARGEMENTS OF THE SPINAL CORD OF THE MOLE-RAT*

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LITERATURE AND PROBLEM

The central and peripheral organs are correlated in their development. The environmental conditions shape the mode of life of an animal and the latter reflects itself in the developmental state of the two organs just mentioned. Concrete illustrations of this principle are already numerous even on the side of the spinal cord alone. In spite of Taft's assertion that amputation at adult age results in no visible reduction of motor cells in the anterior horn of the spinal cord, Elders found that the pertinent lateral cell groups in the horn are either decreased or vanished in case born without a forearm. Curtis and Helmholtz noticed the preservation of the medial motor cells in abrachial monsters, while in the lateral region there are merely scattered a small number of cells. Experimental extirpation of a limb bud at an early embryonic stage induces a degraded growth of the spinal cord and related structures. The operative effects are generally comparable as shown by Shorey and Detwiler in amphibia, by Hamburger in birds and by Hall and Schneiderhan in mammals.

The principle of correlated development of the central and peripheral organs is also corroborated by observations of the internal structures of the spinal cord in animals with the fore and hind legs of disproportionate bulk, as laid out by nature's experiment, so to speak. The porpoise (Phocaena communis) is devoid of hind legs, its fore extremities are transformed into flapers and the tail musculature is greatly overdeveloped. Both Hepburn and Waterston, and Pressly and Cobb reported that its lumbar cord shows no enlargement, the cervical intumescence is still visible, while the motor centres of the tail muscles are very much strengthened. Schmid observed several species of hopping rats (Dipus laculus, Alyctaga saliens, etc.) with

short fore legs and long slender hind legs and found a consistent reduction in the diameter and length of the cervical cord, in its cell groups in control of the fore legs as well as in the volume and quantity of the motor cells themselves. The present writer has been interested in this problem in recent years. The motor cells in the dorsolateral region of the pertinent anterior horn of the spinal cord are increased in the polydactylos mice. This finding has been confirmed by Baumann and Landauer in polydactylos domestic fowls. The fore extremities of the bat are converted into a flying apparatus; the bulk of the spinal motor centres of the "wings" is three times that of the hind legs, as estimated by the writer. In the very rare symphotic fetuses, some muscles in the lower portion of the body are lacking or anomalous; the magnitude of the motor cells in the lumbar enlargement is correspondingly decreased, particularly in the terminal part. As the fore leg of the mole is about three times larger than the hind leg, a similar ratio exists between the sizes of the spinal motor centres of the extremities.

The rodent mole-rat (*Taphozous melanolophus*) is similar to the insectivore mole in many respects. It is subterrestrial in habit; its eyes are minute, yet functional, in contrast to the total blindness of the mole. The latter digs underground tunnel in search of small life, while the mole-rat excavates subterranean vast dome and is omnivorous. The fore leg of this animal is about twice as big as the hind leg. With respect to size, the toes are in the order of 3, 4, 2, 1 (shorter and stouter than 2) and 5 (Fig. 1, A, B), while in the mole they are in the natural order of 1, 2, 3, 4 and 5. The mole digs ahead using chiefly the toes on the radial side, casting the earth outward, whereas the mole-rat employs mainly the three middle toes and scrawls the loosened earth inward and backward.

With reference to the mode of life of the mole-rat and to the sharp contrast in bulk of its feet, the present study attempts to elucidate whether the pertinent motor cells in its spinal cord are developed in correspondence and whether the huge size of the middle toes is reflected proportionately in the volume of the spinal centres of the digital muscles.

**Material**

The two mole-rats used in this study were captured in the suburb of Peking. They were full-grown, number 1 weighing 373 g and number 2, 407 g. The spinal cord was first fixed together with the vertebral column in 10% formalin and later refixed in Bouin's fluid after its removal. The spinal cord was cut into several pieces and embedded in paraffin. Serial sections were cut at 15 micra and stained with cresyl violet. The right fore and hind legs of mole-rat 1 were clipped down for photography (Fig. 1) for an intuitive comparison of the relative bulk of the feet and toes.

The sections of the spinal cord at levels of the cervical and lumbar enlargements, which are connected with the motor nerves for the extremities,
were examined under the microscope for a comparison of the configuration of the gray and white substances, the array of the cell columns and the magnitude of the motor cells. This should provide a basis for judging any probable reflection of the relative sizes of the extremities in the development of their spinal centres. The two series of sections should serve to check each other in the matter of the validity of the material as well as the reliability of the observation.

**Quantitative Comparison of the Motor Cells in the Cervical and Lumbar Enlargements of the Spinal Cord**

*Procedure.* The reader is referred to the report on the spinal cord of the mole\[^{16, 17}\] for a detailed account of the procedure for observing and handling the section material; suffice it to reiterate several essential points. The differentiation of the cell columns in the human spinal cord and their nomenclature are not all appropriate for a slender cord as that of the mole-rat\[^{19, 20}\]; nevertheless, they are still comparable in a general way (Figs. 2—6). The cell columns arranged from the medial to the dorsolateral part of the anterior horn innervate in order, as generally agreed, the muscles of the proximal to the distal portions of the extremity\[^{21, 22}\]. The present study concerns itself first with a comparison of the motor centres of the fore and hind legs in their entirety, so the motor cells on the levels of the enlargements are counted up. The sharp contrast in bulk of the fore and hind legs centres around the feet and the foot muscles are situated mainly below the knee. This fact calls for a separate count of the cells in the posterior part of the horn, including the posterolateral (pl) and retroposterolateral (rp) columns of the human cord, which are regarded as supplying the distal part of the extremity\[^{21—25}\]. The situation in the mole occurs also in the mole-rat that the gray matter of the anterior horn in the enlargements spreads both in anterior and posterior directions. Practically no difficulty exists in dividing the horn into anterior (a) and posterior (p) parts. Those cells scattered in the central area may be arbitrarily assigned to either of the divisions. Finally, the great difference in size of the toes demands a comparison of their controlling cell groups; that is, the retroposterolateral column (rp) dorsal to the posterolateral column. As in the case of the larger columns, this slender one also has subdivisions which are but poorly demarcated, permitting merely a general examination of its cell elements.

For a comparison of the two series of sections it is essential to ascertain at the outset their corresponding levels. The cervical enlargement of the human cord is defined as from cervical segment 5 down to thoracic segment 1 (or 2), in the latter terminating the retroposterolateral column. The caudal end of this column in the spinal cord of the mole-rat is very definite; the portion of 10.8 mm from this plane rostrally roughly comprises the cervical enlargement, which somewhat exceeds the conventional scope of this intume-
scence. The retroposterolateral column in the lumbar enlargement of the human cord extends down to sacral segments 2–3; a distance of 2.4 mm below its terminus is fixed as the caudal extremity of the cord in the mole-rat. Again, 10.8 mm from this plane rostrally embraces arbitrarily the lumbar enlargement, the upper boundary reaching about lumbar segment 1. Within the bounds of the enlargements, beginning with the caudal limit, 18 levels (the last two missing in the lumbar enlargement of mole-rat 2) are picked up at an interval of 0.6 mm, which constitute the corresponding planes in the two series. The motor cells in the anterior horn on these levels are separately calculated (*vide infra*). On this basis, curves are plotted to show the distribution of cells (Figs. 7–8). From each of the enlargements of mole-rat 1, at an interval of 1.2 mm, six sections are taken for photomicrography in the convenience of serially comparing the disposition of the motor cell groups in the two intumescences (Fig. 6). Again, from each of the two regions in the animals a section with the most numerous cells is reproduced by photography at high magnification to illustrate the typical configuration of the white and gray matters, the apportionment of the cell columns, the shape and size of the component cells, *et cetera* (Figs. 2—3, 4—5).

A general survey under the microscope was made of the enlargement portions of the two series of sections. The representative sections were next examined in detail. An off-hand sketch was drawn of the anterior half of the section indicating the situation of the white and gray substances. The cell columns in the anterior horn on the two sides were next delimited and compared with respect to their relative correspondance. The cells in the various columns were then counted up and reproduced faithfully in the sketch. Only somatic motor cells with nuclei were taken into account excluding the visceral motor and other cell varieties in the anterior and lateral horns. The cells included were generally larger and darker stained, with the Nissl bodies in large lumps. In this way, the magnitude of the motor cells was underestimated, but the counts were more useful. An absolute accuracy can hardly be claimed for a cell-counting work; what we should be after are the relative values as a basis for a qualitative statement.

**General Aspects of the Cross Sections through the Two Enlargements.** The cervical and lumbar enlargements of the two series of sections show similar differences in the general appearance. The cervical exceeds the lumbar region in diameter, area and magnitude of gray matter in the anterior horn. However, the contrast is by far moderate in comparison to the situation in the bat*¹³* and mole*,¹⁶,¹⁷*, the fore leg of the latter animals being prodigious in bulk. In the enlargements of the mole-rat, the gray substance of the anterior horn spreads outward as generally in other mammals with extremities comparable in size, yet in the cervical intumescence it protracts too far out ventrally and dorsolaterally, thus producing what Bertrand and Bogaert*²⁷* designated as *angle antéroexterne* (ae) and *angle postéroexterne* (pe). The breadth and length of these angles on the cervical levels outstretch those in the lumbar
region (compare Figs. 2–3, 4–5), the posteroexternal angle in particular. The last-mentioned angle contains one or more clusters of motor cells comprising the retroposterolateral column (rp) which controls the toe musculature. Sometimes only one or two cells present themselves in this locality, yet the tapered angle delineated by the surrounding white matter is still distinct. It is to be noted that the far-stretching of the posteroexternal angle occurs in the middle section of the retroposterolateral column as shown in Fig. 4. This level is caudal to that of Fig. 2, in which the angle is both large and long. As the third and fourth toes of the fore foot are exceptionally large, it seems natural for the middle portion of the pertinent motor column to be hypertrophied in correlation.

Comparison of the Motor Cell Magnitude in the Anterior Horn as a Whole of the Enlargements. By counting up the motor cells in the anterior horn and by averaging the two sides, a representative value was obtained. This was individually done for all the levels of the cervical and lumbar enlargements. The 18 values for each of the enlargements (16 values for the lumbar enlargement of mole-rat 2) were next plotted into curves on the square paper. The two solid lines (ca) in Fig. 7 indicate the distribution of the motor cells in the whole anterior horn of the cervical and lumbar enlargements of mole-rat 1. In Fig. 8 the two solid lines (ca) represent a similar distribution in the two regions of mole-rat 2. The cell magnitude in the cervical enlargement is consistently greater than that in the lumbar enlargement in both cases.

This contrast in cell magnitude may be presented in another way. The average values on the chosen levels of each enlargement were added up. The total sum for the cervical region of mole-rat 1 is 473 cells and that for the lumbar levels, 337 cells, the ratio being 1.4:1. This difference is again reproduced by the length of the vertical bars in Fig. 9. The cervical and lumbar regions are represented by blank (C) and stippled (L) bars respectively. In mole-rat 2, the cervical and lumbar enlargements total 458 and 296 cells respectively, with a ratio of 1.5:1. This proportion is again illustrated by the vertical bars, with blank (C) and stippled (L) bars standing for the cervical and lumbar regions respectively. It is evident at a glance that the cervical surpasses the lumbar intumescence in cell magnitude in both the two cases.

Summing up, as the fore leg is larger than the hind leg in the mole-rat, a correlated difference is manifest in the cell magnitude in the whole anterior horn of the spinal cord, which is responsible for their innervation.

Comparison of the Motor Cell Magnitude in the Posterior Part of the Anterior Horn of the Enlargements. As the disparity in bulk of the fore and hind legs in the mole-rat centres chiefly around the foot, a separate comparison of the cell quantity in the anterior horn, which supply the muscles below the knees, should better reveal a differential reflection on the central side of the relative sizes of its feet. The relevant cell groups in this connection are the
posterolateral (pl) and retroposterolateral (rp) columns, together with some
cells strewn in the central part of the horn. Collectively, these cells may be
designated as forming the posterior part (p) of the anterior horn, which is
often distinct from the anterior part (a).

Following the procedure just stated, the motor cells in the posterior part
of the horn were summed up and averaged for the two sides, thus procuring
a relative value for a particular section. This was repeated for all the selected
levels of the two enlargements. The average values on these levels were
next plotted into curves. The broken lines (pp) in Figs. 7 and 8 signify
the distribution of the motor cells in the posterior part of the horn in the
cervical and lumbar enlargements of mole-rats 1 and 2 respectively. Thus,
the posterior part of the horn, as the centre of the foot muscles, shows consis-
tently a higher distribution of motor cells in the cervical enlargement, a
fact more clearly borne out than a comprehensive comparison of the cells
in the whole horn.

The disproportion in the total cell counts for the two enlargements is
next illustrated in terms of the relative length of the vertical bars in Fig. 9.
In mole-rat 1, the motor cells in the posterior part of the horn at the 18
levels of the cervical enlargement total 277; the number shrinks to 126 for
the lumbar enlargement, presenting a ratio of 2.2 : 1. The two values are then
examplified by the vertical bars. The transverse hatchings (C') stand for
the cervical region and the oblique hatchings (L') for the lumbar region.
Again, in mole-rat 2, the sum total of cells in the cervical region is 260 and
that of the lumbar region is as low as 91, with a ratio of 2.8 : 1. The bars
hatched by transverse (C') and oblique lines (L') in Fig. 9 indicate the
relative values for the cervical and lumbar enlargements respectively. The
bars are more illustrative than the curves that the posterior part of the horn
contains more cells in the cervical than the lumbar enlargement.

Comparison of the Motor Cells in the Posteroexternal Angle of the Anterior
Horn in the Cervical and Lumbar Enlargements. It is generally agreed that
the retroposterolateral column (rp) gives off fibres to supply the digital muscles.
A comparison of the length of this column, its traits in cross section and its
cell magnitude should reveal to better advantage any reflection on the central
side of the relative bulk of the toes on the fore and hind feet. But here exists
insurmountable difficulty. This column lies dorsal to the posterolateral
column (pl), from which it is but poorly separated. Both columns contain
ill-defined subdivisions; it is impossible to calculate the cell elements properly
of any one column.

The retroposterolateral column in the cervical enlargement of mole-rat
1 is approximately 6.6 mm long in terms of sections, while it measures 3.6
mm in the lumbar region, with a ratio of 2 : 1. As this column is slender at
the lumbar levels, its length constitutes no good measure of its volume. The
incompleteness of sections in the caudal end of the lumbar cord prevents a similar estimate for mole-rat 2. In the middle section of the cervical enlargement (Fig. 4, rp), this locality contains more cells and thrusts far outwards to taper into a posteroexternal angle (pe). On the other hand, this column in the lumbar region is represented by a dorsolateral dispersion of a few cells, forming no sharp angle. An attempt was made to compare the cell elements within this angle on the cervical levels. The cells in the middle section of this column are generally greater in number and bulkier in volume; exceptions are many, however. On the whole, it may be said that the retroposterolateral column which controls the toe muscles is by far better developed in the cervical than in the lumbar cord.

To sum up, in the two mole-rats the cervical surpasses the lumbar enlargement in the development of the somatic motor centres. This conclusion is borne out by a comparison of the cell magnitude and other traits in the whole anterior horn, in its posterior part and in its posteroexternal angle. The development of the leg, foot and toe muscles is thus differentially reflected in the morphology of their spinal centres.

**Discussion**

**Correlated and Commensurate Development of the Central and Peripheral Structure.** Beside the mole-rat, there exist other mammals with the fore leg excelling the hind leg in bulk, most notably the bat and the mole on which I have made separate reports. The fore extremities of the bat are transformed into a powerful flying organ; the cell magnitude in the anterior horn in control of the fore leg is three times that of the hind leg. Again, the fore leg of the mole is three times larger than its hind leg; a similar ratio is found between the motor cells innervating them. In the case of the mole-rat, the disparity in size between the fore and hind legs is more moderate, being about 2:1; a corresponding but lesser difference is present in the cell magnitudes supplying the extremities. Moreover, in the mole-rat, the posteroexternal angle of the horn, which contains the cells in control of the digital muscles is smaller than that in the mole. In general, the gray matter of the anterior horn and the musculature of the leg develop in association and, furthermore, in commensuration.

**Site of the Spinal Centres of the Digital Muscles.** Anatomical, embryological and pathological facts hint that the retroposterolateral column gives off fibres to the muscles of the fingers or toes. It is not yet clear how the motor cells for the five digits are arranged within this column. In light of embryological data, the centre for the first digit should be situated in its rostral part. As the big toe of the mole comprises practically a lesser half of the fore foot, it is but natural for this fact being reflected specifically in the retroposterolateral column. The material on hand testifies to the greater volume of the rostral end of this column and to the clearer demarcation of its
subdivisions.\textsuperscript{16, 17} As the third toe on the fore foot of the mole-rat ranges the largest, and next comes the fourth, it may be reasonably inferred that the middle section of this column should be better developed. In the cervical enlargement, the middle portion of this column actually stretches far out, tapering into a posteroexternal angle, and, further, the cell elements here are generally larger and more numerous. However, the evidence is still inadequate for localizing at his plane the spinal centres of the third and fourth toes.

It is no easy matter to localize accurately the spinal centres of the separate digits. Of course, it can be done to divide first the motor nerves to the toes and examine the subsequent chromatolysis of the pertinent motor cells in the anterior horn after a lapse of time. This method has certainly accomplished very much in identifying the spinal motor cells for the striate muscles of the trunk and extremities, yet its fallibility is now too well known. Marinesco\textsuperscript{28}, de Nervo\textsuperscript{29}, Le Gros Clark\textsuperscript{30} have shown successively that only a vigorous sectioning of the proximal part of a motor nerve is capable of producing a conspicuous chromatolysis of the relevant cells. In case the cutting is near the muscle innervated, the deteriorating effect is slight or nil. On the positive side, Gehuchten and Buck\textsuperscript{135} reported that consequent to the severance of the sciatic nerve at its exit, the chromatolyzed cells are focussed at the posterior part of the anterior horn. Thereupon they inferred that this locality embodies the spinal centres for the shank and foot muscles. Again Romanes\textsuperscript{124} cut the median and ulnar nerves at the wrist of the rabbit; chromatolysis was brought about only in the cells of the retroposterolateral column (his column 10), extending from cervical segment 8 to thoracic segment 2. He then regarded this column as innervating the foot muscles. Moreover, Reed\textsuperscript{51} sectioned the median, radial and ulnar nerves of the monkey at the shoulder; the degenerated cells induced by the transected median nerve are situated in the dorsal part of the posterolateral column and the middle part of the retroposterolateral column; the division of the radial nerve was followed by the deterioration of cells at the rostral levels of these two columns; and finally, the severance of the ulnar nerve resulted in chromatolysis of cells at their caudal planes. Thus, the results indicate that the upper parts of these columns supply the big and the radial digits, while the little and the ulnar toes are innervated by their lower parts. The situation in the mole-rat is in general agreement with these findings. This problem waits further elucidation.

**SUMMARY**

The mole-rat inhabiting the vicinity of Peking has its fore foot twice as large as its hind foot. Serial sections of the spinal cords of two adult animals were compared as to the configuration of the white and gray substances and to the relative magnitudes of the motor cells in the anterior horn of the cervical and lumbar enlargements with the following results.
The cervical enlargement innervating the fore leg is much larger in cross section than the lumbar enlargement which innervates the hind leg. As compared to the lumbo-sacral levels, the anterior horn of the cervical region is broader in area and its cell columns are bulkier in volume and clearer in demarcation. The gray matter of the horn stretches outward to form the anterouteral and posterouteral angles. The latter, in particular, thrusts far out and contains the retroposterolateral column supplying the digital muscles.

At equally spaced representative levels, the cervical enlargement consistently out-ranks the lumbar enlargement in the distribution of the motor cells in the anterior horn as a whole, which controls the leg musculature. Again, the sum total of such cells at all the levels of the cervical enlargement is 1.4—1.5 times that of the lumbar enlargement. Moreover, when taken separately, the total motor cells in the posterior portion of the horn of the cervical enlargement, which innervates the distal muscles of the enormous fore leg, are 2.2—2.8 times those of the lumbar enlargement.

The third and fourth toes assume enormous size on the fore foot. The retroposterolateral column which supplies the digital musculature is larger and longer in the cervical enlargement. The cells in the middle segment of this column are generally greater in bulk and in number, and with better defined subdivisions. These traits apparently hint that the motor cells in control of the third and fourth toes are mainly located at this plane.

The striking disparity in the size of the fore and hind feet of the mole-rat reflects itself in a differential development of the anterior horn cells in the cervical and lumbar enlargements. That the motor centres of the spinal cord develop in correlation and commensuration with the peripheral organs innervated as well as with the particular mode of life of the animal is thus demonstrated once more.

References


*Quoted in [24].