Department of Anatomy, University Medical School, Pécs
(Director: Prof. J. SZENTÁGOTHAI)

SOMATOTOPIC ARRANGEMENT OF SYNAPSES OF PRIMARY SENSORY NEURONS IN CLARKE'S COLUMN

J. SZENTÁGOTHAI

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Some years ago the synapses of Clarke's column have been analyzed with experimental morphological methods by the author and ALBERT [6]. Three types of synapses have been described. (i) Large muscular afferent primary neurons establish very large and long parallel contact synapses with the Clarke neurons, which finally terminate in unusually large terminal knobs; they have been called "giant synapses". (ii) Another type are terminal knobs of ordinary size, the preterminal fibres of which reach the Clarke neurons mostly at right angles. Their intraspinal origin had been established in the paper mentioned, but as has been pointed out later [3] they are not recurrent collaterals from the dorsal spinocerebellar tract (DSCT), as supposed originally, but originate from spinal interneurons situated in the lower lumbar segments. (iii) A third type of synapse also from spinal interneurons is established by a meshwork of extremely fine fibers in close connection with the Clarke neuron surface. This type of synapse has recently been brought into connection with inhibition [5] exerted by spinal interneurons upon Clarke neurons as first shown by LAPORTE, LUNDBERG, and OSCARSSON [2], and investigated more exactly with the intracellular microelectrode technique by CURTIS, ECCLES and LUNDBERG [1]. — These three histological types of synapse fit fairly well with the physiological findings of the LUNDBERG group in Lund, according to which besides the direct monosynaptic action of predominantly muscular afferents, Clarke neurons are impinged upon by excitatory and inhibitory influences from spinal interneurons.

During more recent investigations on the intraspinal course of primary sensory neurons with the NAUTA technique an interesting somatotopic arrangement of primary sensory neuron synapses in Clarke's column has been noticed, a short account of which shall be presented in this paper.

Material and methods

The investigations were carried out on cats in which the dorsal roots L_3, L_4, L_5, L_6 and L_7 were transected separately. The cats were let to survive for 5 days. The spinal cord was fixed by perfusion with neutral formol and investigated in frozen sections according

to NAUTA's method. Transverse sections were prepared from each segment below Th_9, but the adjoining parts of the segments Th_{13}—L_1 and L_{2-3} were spared for longitudinal sectioning. Care was taken for exact orientation of the longitudinal sections in order to get the Clarke columns of both sides as far as possible into the same slides.

Results and conclusions

As known, primary sensory neuron collateras do not enter Clarke's column at the level of their entrance into the cord, but have to ascend for one or two segments in the dorsal fasciculus. This is of course natural in case of sensory neurons of the segments below L_4, where there is no Clarke column. From tracing of degenerated fragments after transection of the dorsal roots L_{3-4} it appears, however, that L_4 collaterals do not enter the column below L_2, and L_3 collaterals not below L_1. — The distribution of collaterals originating from a given segment (*e. g.* L_4) can best be understood from the schematic diagram on Fig. 1. Clarke's column is represented by a vertical cylinder with the nerve cells also oriented longitudinally, *i. e.* with long axes parallel to the axis of the spinal cord. After transection of the dorsal root L_4 signs of degeneration are found in the column between the segments L_2—Th_{10} within a well-defined space limited between two parallel nearly sagittal planes, slightly sloping upwards in medial direction. The distance of the planes from another is about a quarter of the diameter of Clarke's column or somewhat less in the case of the small roots from L_4 upwards, and considerably larger — to about half of the diameter in the case of the larger roots L_6—S_1. This means that direct dorsal root collaterals after having entered Clarke's column are shifted during their ascent gradually in medial direction, establishing thus synaptic contact with more and more medially situated Clarke neurons. Since, as has already been stated [6], collaterals from the different roots do not enter Clarke's column at the same level, this distribution of collaterals is not due exclusively to a medial shifting of collaterals inside the column but also to a similar shift of the ascending white dorsal column fibres. In sagittal sections of the cord of animals with previous lumbar radicotomy one encounters degenerated collaterals entering the gray matter from the dorsal fasciculus in large numbers as high as five or six segments above the level of the entrance of the sectioned root into the spinal cord. These collaterals are situated the more medial the higher they are above their segment of entrance.

However well defined the borders of the space in which the collaterals arising from any dorsal root are distributed in Clarke's column, these borders do not separate the distribution fields of two neighbouring or any other segments. On the contrary, there is a considerable overlap between collaterals of neighbouring segments. The collaterals derived from the large lower lumbar segments overlap not only with their adjacent, but even with the next and perhaps even more segments. This is demonstrated diagrammatically in Fig. 2,

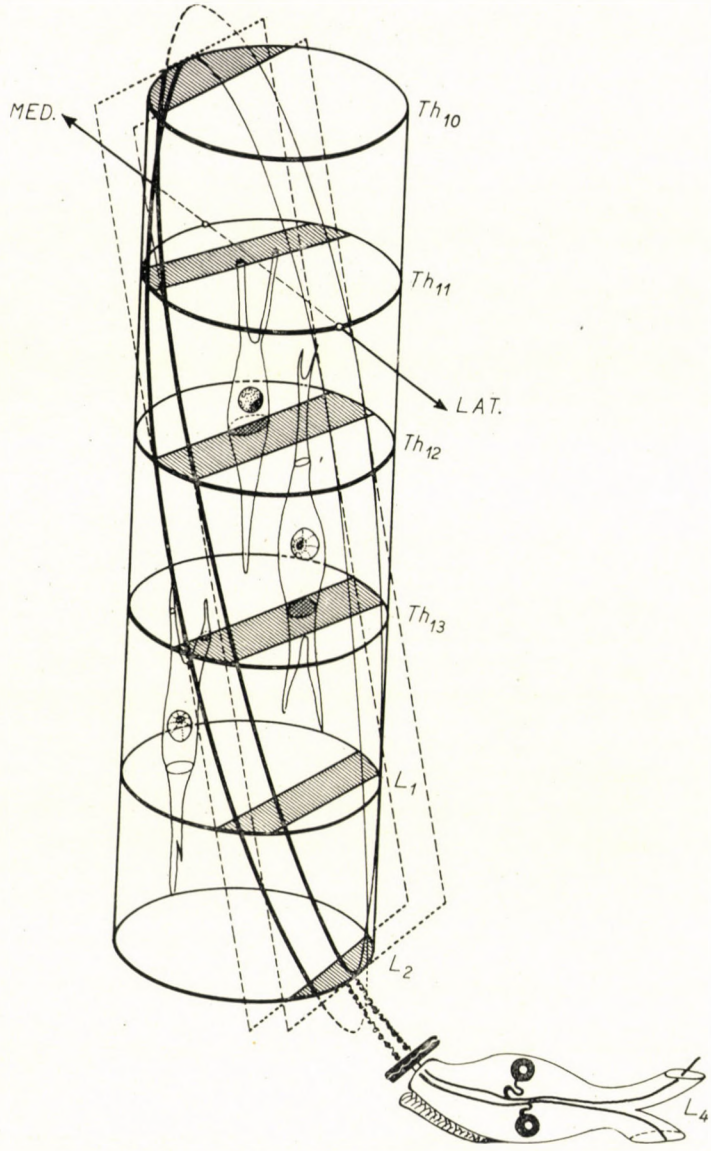

Fig. 1. Diagram showing the distribution of primary sensory collaterals in Clarke's column originating from the segment L_4. Further explanation in the text

with indication of the "giant (parallel contact) synapses" involved. — Thus it appears that synapses between primary sensory neurons of different segments with Clarke neurons are situated in parallel oblique slices of the column sloping upwards in medial direction and showing considerable overlap between neighbouring and even more distant segments.

The significance of this somatotopic arrangement of synapses would better be understood if we had more exact information on: (i) the distribution and termination of the distal branches of the neurons of a given segment which terminate in lower or upper parts of the column, and (ii) on the mode of termination of DSCT fibers in the cerebellum arising from different levels of Clarkes column. Unfortunately we do not know anything about these questions. Since according to LUNDBERG and OSCARSSON [3] most DSCT neurons are monosynaptically stimulated either by muscle spindle (I*a*) or Golgi tendon organ (I*b*) afferents, the possibility must be taken into account that the one of the two types might be localized more caudally than the other. This has already been tested experimentally by OSCARSSON [4] with descending longitudinal sectioning of the spinal cord to interrupt the Clarke neuron axons successively as they enter Flechsig's fasciculus. Since the discharges due to I*a* and I*b* stimulation decreased concomitantly in such experiments, this possibility has been ruled out. So we must suppose that Clarke neurons which are monosynaptically activated by I*b* afferents are situated in the same level as those impinged upon by I*a* afferents. — The mode of termination of dorsal spinocerebellar fibres originating from different levels of the cord is a question that remains to be investigated by appropriate methods.

Summary

The synapses of primary sensory collaterals of lumbar segments with Clarke neurons are situated in parallel oblique slices of the column sloping upwards in medial direction. There is considerable overlap in Clarke's column between the synaptic territories of neighbouring segments. In consequence of this arrangement the Clarke neurons monosynaptically excited by the primary sensory neurons of a given segment are generally the most lateral ones in the lower and the most medial ones in the upper part of the synaptic territory of that segment in Clarke's column.

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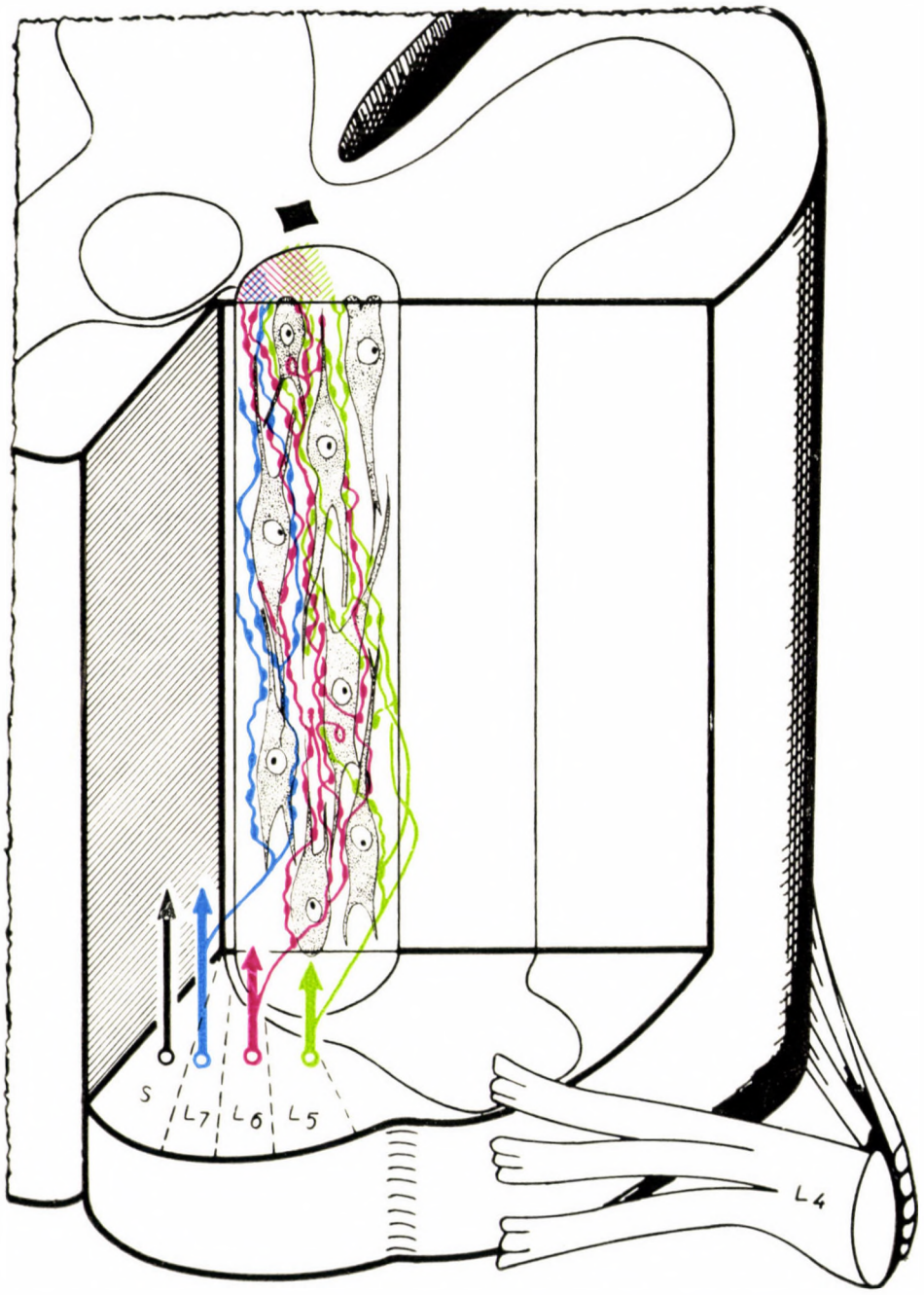

Fig. 2. Distribution and overlap of primary sensory collaterals derived from the segments L_{5-7}

СОМАТОТОПИЧЕСКОЕ РАСПРЕДЕЛЕНИЕ СИНАПСОВ ПЕРВИЧНЫХ ЧУВСТВУЮЩИХ НЕВРОНОВ В СТОЛБЕ КЛАРКЕ

Й. СЕНТАГОТАИ

Первичные чувствующие невроны поясничных срезов образуют в столбе Кларка в цилиндрических сегментах, разграниченных косыми, в верхнем направлении медиально наклоняющимися плоскостями, синапсы с находящимися в этих пространствах Кларковыми нервными клетками. Между подобными синаптическими областями соседних срезов наблюдается значительное совпадение. В результате этого распределения происходящие из определенного корня коллатерали образуют в нижней части относящейся к данному корню области непосредственные синапсы с боковыми, а в верхней части этой области с медиальными клетками Кларка.

SOMATOTOPISCHE ANORDNUNG DER SYNAPSEN VON DEN PRIMÄREN SENSORISCHEN NEURONEN IN CLARKESCHEN SÄULE

J. SZENTÁGOTHAI

Die Synapsen zwischen den primären sensorischen Neuronen der Lumbalsegmente und Clarkeschen Zellen sind in schiefen nach oben medialwärts geneigten durch parallele Ebenen begrenzten Zylinderschnitten der Clarkeschen Säule lokalisiert. Die zu benachbarten Segmenten gehörenden Scheibenterritorien der Clarkeschen Säule überdecken sich weitgehend. Dieser Anordnung zufolge werden durch die Kollateralen jeder Dorsalwurzel im kaudalen Verteilungsbereich der Clarkeschen Säule laterale, im kranialen Verteilungsbereich mediale Nervenzellen direkt erregt.

Prof. Dr. János SZENTÁGOTHAI, Pécs, Dischka Gy. u. 5. Hungary