Variations in the Form of the Golgi bodies during the Development of Neurones.

By

A. Subba Rau, B.A., M.Sc. (Lond.), F.R.M.S.,
Derby Scholar, Department of Zoology and Comparative Anatomy,

and

R. J. Ludford, Ph.D. (Lond.), F.R.M.S.,
Department of Embryology and Histology, Institute of Anatomy, University College, London.

With Plate 39.

A. Introduction.

The form of the Golgi apparatus, or body, varies considerably in different cells. In certain cells of insects it has the form of scattered granules or rodlets more or less evenly distributed throughout the cytoplasm (**11**). In molluscs, such as Helix and Patella, it consists of crescentic rodlets, either grouped together or scattered throughout the cell (**7, 8**).

The Golgi body in the cells of the higher vertebrates appears to be of a more fluid consistency than in the lower animals, which makes it a matter of difficulty to determine whether the apparatus in such cases consists of a network, or of fused rodlets. In the cells of the adult spinal ganglion of such organisms it has a reticulate appearance with the normal silver impregnation, but with less intense impregnation it can in many cases be seen as separate rodlets. Whether the network-like appearance is due to coalescence of the separate semi-fluid rodlets cannot properly be determined with our present technique. The probability of variation between network and separate rodlets, during differences of the colloidal conditions of the

cell under varying functional activity, must be borne in mind (**10**). In most mammalian epithelial cells the Golgi body has the appearance of a closed network at the proximal end of the cells external to the nucleus (**5**). During mitosis the network breaks up into separate rodlets, which are re-formed into other networks or groups of rodlets around the centrosome, during the telophase. The apparatus usually retains its connexion with the centrosome and archoplasm; but in ciliated epithelium, such as that of the epididymis of the mammalia, the centrosome is associated with the cilia, and the Golgi body occupies a position in the cell between the centrosome and the nucleus. In gland-cells during secretion several investigators have described an enlargement and subsequent disintegration of the network. Opinions vary as to whether the substance of the apparatus contributes to the formation of the secretion (**12**).

A certain amount of experimental work has appeared on the Golgi body in nerve-cells. It has been shown that starvation has apparently no influence on it; but exposure to cold causes contraction of the apparatus round the nucleus (**4**). Section of the axon branch of a ganglion cell results in the dispersal of the network to the periphery of the cell, together with a certain amount of dissolution, but the network is reconstructed ultimately after recovery (**13**). It has been suggested that the dispersal of the apparatus during mitosis and periods of functional activity is related to the higher degree of metabolic activity of the cell (**10**).

Recently, the view that the sympathetic nervous system is derived from the central nervous system, and that the medullary substance of the suprarenal body is formed from cells of the primary sympathetic nervous system, has been confirmed (**15**).

The present research was carried out with a view to investigating the form of the Golgi apparatus in the neurones of the central nervous system during development, and also to find out what cytological differences existed between the embryonic neurones and the cells of the adrenal bodies of nervous origin. It has not been our aim to describe the cytology of the nervous

system during ontogeny, but rather have we confined our attention to the general morphological changes undergone by the Golgi body in nerve-cells.

B. Material and Methods.

The material used in this work consisted of chick embryos incubated for various lengths of time. The younger embryos were fixed whole by Da Fano's cobalt nitrate method, and by the Mann-Kopsch osmic method. At the suggestion of Professor J. P. Hill, thorium nitrate was tried as a substitute for cobalt nitrate. This gave a better protoplasmic fixation, but the Golgi apparatus was not so well demonstrated. Phosphotungstic acid (1 per cent. in distilled water) was also tried, but this gave dense precipitation of the cell proteins, without any distinguishable Golgi impregnation on after-treatment with the silver impregnation method of Cajal.

With advanced embryos and with the adult, the spinal ganglia were dissected out after a preliminary fixation of portions of the vertebral column. Except for this treatment, the method adopted was the same throughout.

After paraffin sections had been cut, the silver impregnated sections were toned and stained, either with neutral red containing only a trace of glacial acetic acid, or with toluidin blue.[1]

C. The Golgi Body of the Neurones of the Spinal Ganglia.

In the spinal ganglion cells, and in the cells lining the neural canal of the four-day chick, the Golgi apparatus forms a compact structure by the side of the nucleus. In the silver-impregnated sections it has the form of a dense mass of granules or rodlets (fig. 2, Pl. 39), and it is difficult to distinguish individual rodlets. However, with the osmic-acid preparations of the same age, at one side of the nucleus there is to be seen a slightly osmicated area, within which the Golgi rodlets or

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granules are visible (fig. 1, Pl. 39). This zone of partial osmication is probably of the same nature as that described recently by Brambell (1) in the neurones of the snail (Helix).

At a slightly later stage, in the chick embryo of seven days, cells of the spinal ganglia are larger and the Golgi apparatus is also relatively larger; however, it still partakes of the nature of a cluster of coiled rodlets or aggregated granules applied to one side of the nuclear membrane (fig. 3, Pl. 39). In the neurones of the spinal cord, and of the spinal and sympathetic ganglia, the primitive form of the Golgi apparatus is a compact cluster of bodies grouped to one side of the nucleus. At a varying stage in each, a process of scattering of the apparatus takes place, but it does not occur at the same time in all cells. The process is evidently a slow one. The transition stage is shown in the cells of the ventral horn of the spinal cord of a chick of fourteen days. As can be seen in fig. 4, Pl. 39, the apparatus which at this stage is somewhat net-like in form has almost come to surround the nucleus. However, a complete network throughout the cytoplasm is not yet established.

Within the cells of the spinal ganglia of the newly born chick three forms of the apparatus can be distinguished. In the largest cell, fig. 5, *a*, Pl. 39, it forms a complete network surrounding the nucleus. In other cells such as are shown in fig. 5, *b*, Pl. 39, the apparatus forms a network closely applied to the circumference of the nucleus, while in the smallest cells, fig. 5, *c*, Pl. 39, it appears to be composed of numerous rodlets seemingly grouped round the centrosphere and extending around the nuclear membrane. The general impression, from a study of the apparatus at this stage, is that there is taking place a gradual spreading of the rodlets throughout the cytoplasm, and that these rodlets are branching out and anastomosing to form a network; however, we have borne in mind the possibility of such variations as are shown in this figure being due to differences in the plane of section of the cells, and also to slight variations in the degree of impregnation with the silver. Although these differences in the appearance of the apparatus are distinctly seen in the preparations, yet we have

not observed the small compacted groups of rodlets characteristic of the earlier stages.

The Golgi body in the spinal ganglia cells of the adult has the characteristic net-like appearance. In all the larger cells the network completely fills the cytoplasm, as is shown in fig. 6, Pl. 39. In some of the smaller cells the network is more limited in its distribution throughout the cytoplasm.

D. The Golgi Body in the Neurones of the Sympathetic Ganglia.

The same general sequence in the development of the Golgi apparatus is to be observed in these cells as has been described in those of the central nervous system. In the early stages the apparatus forms a cluster of bodies at the side of the nucleus, while in the adult the network is established as is shown in fig. 7, Pl. 39, drawn from a section of the coeliac ganglion.

E. The Golgi Body in the Suprarenal Body.

As was mentioned in the introduction, according to Rau and Johnson (**15**) the medulla is derived from the so-called primary sympathetic nervous system by the (outward) migration of cells. In fig. 8, Pl. 39, are shown three of the cells of the medulla of the suprarenal body of the adult. It will be observed that the apparatus presents the appearance of a closed network, or group of coiled rodlets, at one pole of the nucleus, and thereby closely resembles the apparatus in the neurones at early stages of development. In the cells of the cortex the apparatus also appears as a coiled network applied to the nuclear membrane (fig. 9, Pl. 39).

Discussion.

From the observations we have made on the form of the Golgi apparatus in the neurones it appears evident that in the course of development of the cell it begins as a cluster of rodlets, or granules, or as a closely coiled network situated at the side of the nucleus. As development proceeds the Golgi

body gradually spreads out in the cytoplasm, until it comes to form in the large ganglion cells a network-like structure scattered throughout the cytoplasm. In view of the nature of the methods used for the impregnation of the Golgi body, we do not attach much significance to the exact form which it takes. Both our osmic impregnated and silver impregnated material agree as far as general distribution throughout the cytoplasm is concerned. Whether the apparatus appears as rodlets or granules, or as an anastomosing series of rodlets, or even as a complete network, in all probability depends upon the degree of impregnation. One of us has shown in a paper under publication that in tumour cells the apparatus can be impregnated, either as a coiled network, or as a group of curved rodlets. The general distribution of the apparatus throughout the cytoplasm is the same in each case ; but the exact detailed structure is dependent upon the degree of impregnation. We therefore emphasize the fact that such differences in appearance as are shown in fig. 5, Pl. 39, are probably due in a large degree to the nature of the impregnation with the silver. Bearing in mind the limitations imposed by the technique, we feel justified in maintaining that the gradual dispersion of the apparatus during development is an indication of a fundamental cytological process. Owing to the occasions on which the scattering of the apparatus has been observed, viz. during growth of the oöcytes (**7, 8**), in mitosis, and during secretory activity, we conclude that the scattered character of the apparatus in ganglion cells, which is slowly attained during ontogeny, is an indication of the high degree of metabolism existing in those cells during adult life.

It is of interest to note that these observations substantiate from a cytological point of view the opinion of Rabl (**14**), who maintains that the medullary cells of the suprarenal body represent nerve-cells retarded in their development. Comparison of our figs. 1–3, Pl. 39, of the spinal ganglion cells of young chicks with fig. 8, Pl. 39, of medullary cells of the suprarenal body of an adult fowl, shows that the form of the Golgi apparatus is almost identical. It seems possible to

assume that the medullary cells have been derived from the nervous system at an early stage, before the apparatus has become scattered, as we find that the adrenal bodies become established before the scattering of the apparatus has taken place in the neurones. We would, however, emphasize the fact that it is probably more an expression of the functional activity of the cell than an indication of its ontogenetic origin.

Summary.

1. In the spinal ganglia of the chick of four days the Golgi apparatus or body is in the form of a cluster of granules or rodlets, grouped around the centrosphere, at one side of the nucleus (fig. 1, Pl. 39).

2. In a seven-day chick the Golgi body has increased in size and has begun to spread farther around the nucleus (fig. 3, Pl. 39).

3. All ganglion cells examined, both those of the spinal cord and of ganglia, have the Golgi apparatus in this compacted form during their early stage.

4. At a certain period which varies in the different cells the apparatus spreads out in the cytoplasm (fig. 4, Pl. 39), so that in the adult ganglia the apparatus is more or less scattered throughout the cell (figs. 5, 6, and 7, Pl. 39).

5. It is uncertain to what extent variations in the form of the apparatus, whether reticulate or in the form of individual rodlets, are due to differences in the degree of impregnation with the silver. The plane of the section is also an important factor in determining the appearance presented by the apparatus.

6. The medullary cells of the suprarenal body, which are derived from the central nervous system, have the apparatus in the form of a coiled network or cluster of granules at one pole of the nucleus, similar to the cells of the spinal ganglia at the early stage of development.

7. It is suggested that the scattered form of the Golgi apparatus in adult ganglion cells is an expression of the high degree of metabolism existing in these cells.

EXPLANATION OF PLATE 39.

All the drawings have been made by means of a camera lucida with the paper at table level. The objective used was $\frac{1}{12}$ oil immersion Koritska in combination with an 18 compensating eye-piece.

PLATE 39.

Fig. 1.—Group of cells of the spinal ganglion of the cervical region of a four-day chick, showing the compacted form of the Golgi apparatus. (Fixation. Mann-Kopsch, counterstained with acidulated neutral red.)

Fig. 2.—Another group of cells from a similar ganglion prepared by the Da Fano technique.

Fig. 3.—Two cells from the spinal ganglion of a seven-day chick, showing an increase in size of the Golgi apparatus. (Fixation. Da Fano, toned and stained with neutral red slightly acidulated.)

Fig. 4.—Three cells of the ventral horn of the spinal cord of a fourteen-day chick, showing the dispersal of the apparatus. (Preparation same as fig. 3.)

Fig. 5.—Three cells of the spinal ganglion of the new-born chick, showing variations in the form of the apparatus. (Preparation. Da Fano, toned and stained with toluidin blue.)

Fig. 6.—Spinal ganglion cell of the fowl, showing the scattered form of the Golgi apparatus. (Preparation as in fig. 5.)

Fig. 7.—Cell of the sympathetic ganglion of the fowl, showing the Golgi apparatus scattered throughout the cytoplasm. (Preparation same as previous one.)

Fig. 8.—Three cells of the medulla of the suprarenal body of the fowl, showing the Golgi apparatus as a coiled network at one side of the nucleus. (Preparation as before.)

Fig. 9.—Two cells of the cortex of the suprarenal body, showing the Golgi apparatus in the compacted form, drawn from the same preparation as fig. 8.

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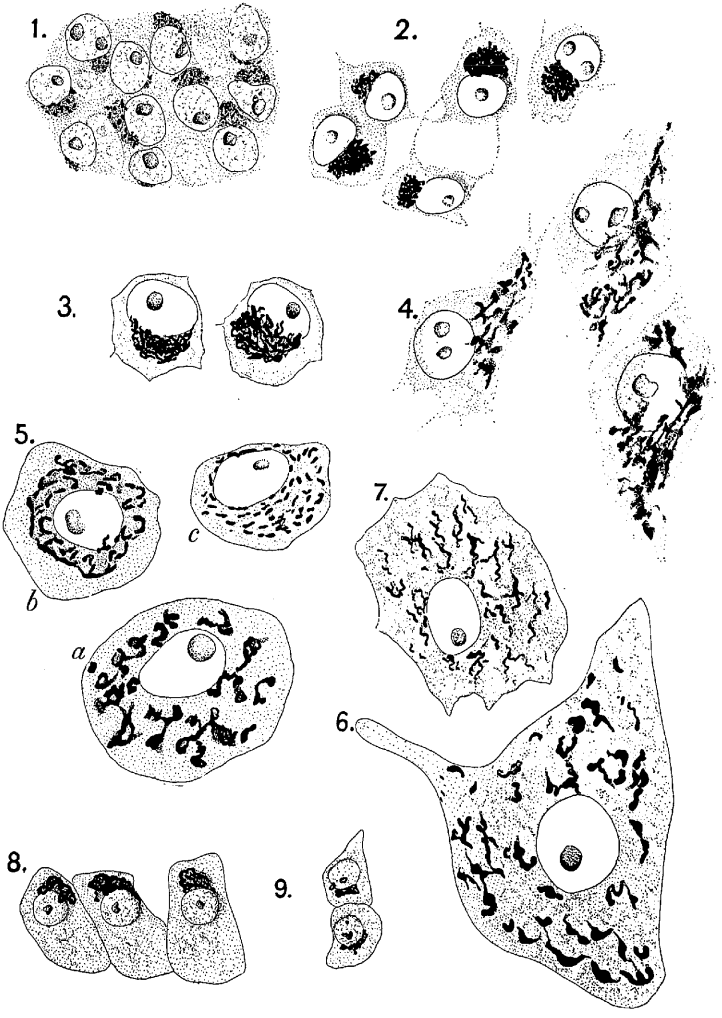
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