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SPECIAL MITOCHONDRIAL TRANSFORMATION IN THE INNER SEGMENT OF VISUAL CELLS

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Abstract

The fairly dense mitochondria in the inner segment of one type of visual cell in the retina of a 6 to 8 days old chick form a close association with large lipid droplets. Another type of visual cell is without lipid droplets. Their granular central substance derives from the breakdown the mitochondria. Apart from mitochondria, the appearance of vesicules and granules and the ribbon lath was also observed in the young visual cells by the authors.

Introduction

Knowledge of the retina of animals standing taxonomically at widely different levels of advancement has been brought about by a large number of light- and electron-microscopic morphological, histochemical and experimental physiological investigations. Valuable handbooks and compendia by BLOOM and FAWCETT (1964), DOWING and BYKOTT (1963), EAKIN (1963), POLYÁK (1957), De ROBERTIS (1969), VILLEGAS (1960) are available to those who are interested in the very complicated process of the mechanism of vision. Yet, it should be stated that there are several unsolved problems in its physiology. Very different theories have emerged on the question of colour vision. Knowledge of the characteristics of the photoreceptor cell structure is very defective and uncertain, as it is almost everywhere in want of a morphological basis. On the basis of our investigations, we want to describe, with some pictures, a pecularity of receptor cells perceiving the first signs of light or colour in a very early phase of the post-embryonic development: mitochondrial transformations in the inner segment.

Materials and Methods

The material of our investigation is the visual cells of the retina of 6—20 days old chicks. After removal of the eye, the retina was removed from the concentric outer coats with a lancet. 0.5—1 mm pieces of retina cut from the equatorial plane, after being prefixed in glutaraldehyde, were fixed with 1 percent osmium tetroxide, buffered according to Milloning. After being dehydrated, they were embedded in araldite. Sections were made, with the aim of culting in the tangential direction, by setting a Tesla BS 478 electron microtome according to the results of semi-thin sectioning. Photographs were made with a BS 500 electron microscope.

Results

The cross-section of the retina of the young chick is very narrow. The stratification of its structure can be observed only with difficulty. The structural density of

the plexiform layers and the lack of pigmentation are the more important differences from the state in the adult animals.

In our examined material differences within, visual cells are striking in the semi-thin sections, and even more in the photographs from low magnification (Fig. 1–2). The distal part of the visual cells is a peripheral photoreceptive lamellar termination, well-demarcated from the inner segment which is rich in mitochondria and named the oval body.

In the early phase of development, these segments of visual cells, show another structure than in adults well-known from the literature.

The visual cells are close to one another: there is no connection between them. The transversely flattened light-receiving lamellae are fewer in the rod cells than in the cone cells but they are more protruding than in the cone cells (Fig. 1, 2, above). Between the lamellar systems the processes of the pigment epithelium are easily visible but they contain no pigment granules. The difference between the inner segments of the distal processes of visual cells is the most striking. The rod cells in the inner segments have lipid droplets of remarkably large size. The diameter of the lipid droplets vary (7–800 nm). Very many mitochondrion was always to be seen in their oval body. The visual cell rich in broad lipid droplets and long situated mitochondria in its inner segment is the rod cell, according to the data of De ROBERTIS (1958), COHEN (1961), NILSSON (1964), VILLEGAS (1960). The young chick has quite other characteristic ultrastructural organization in this cell.

The other visual cell to be seen in the lower part of the picture (Fig. 1–2) is most easily distinguished by the lack of inner-segment lipid droplets. On the basis of this peculiarity and published data, these cells in the oval body rich in mitochondria and can be distinguished by their large nucleus in the cell, by their wider perikaryon and wider proximal central process, we designated them as cone cells.

The differences of visual cells seems to be connected with the age. The functional mechanisms commencing from the visual cells particularly called attention to the formation of mitochondria. In the inner segment of both types of visual cell, there are several mitochondria, as in the visual cells of man and mammals generally. But the facts that the mitochondria are arranged perpendicularly to the longitudinal axis of the segment and that gaps are to be seen in the longitudinal arrangement, do not present themselves at all in the visual cells of the young chicken. The shape and density of the mitochondria of scattered situation remarkably differ in the inner segment.

Rod cell

In case of the rod cell, as seen in photograph 2, above and even more clearly in the subsequent photograph (Fig. 3), the mitochondria which are of nearly identical diameter, form a mitochondrial grouping in the peripheral part of the inner segment.

The mitochondria of the inner segment of the rod cell, investigated carefully, show well limited double membranes. The inner membrane does not show any crista-like intussusception. Rather the matrix of the mitochondrion is filled in with a formation of tubuli touching both side-walls of the mitochondrion. These mitochondria may be as shown in our picture, in a close physiological connection with the lipid droplet (Figs. 2–4). It is often to be seen that one or other mitochondrion

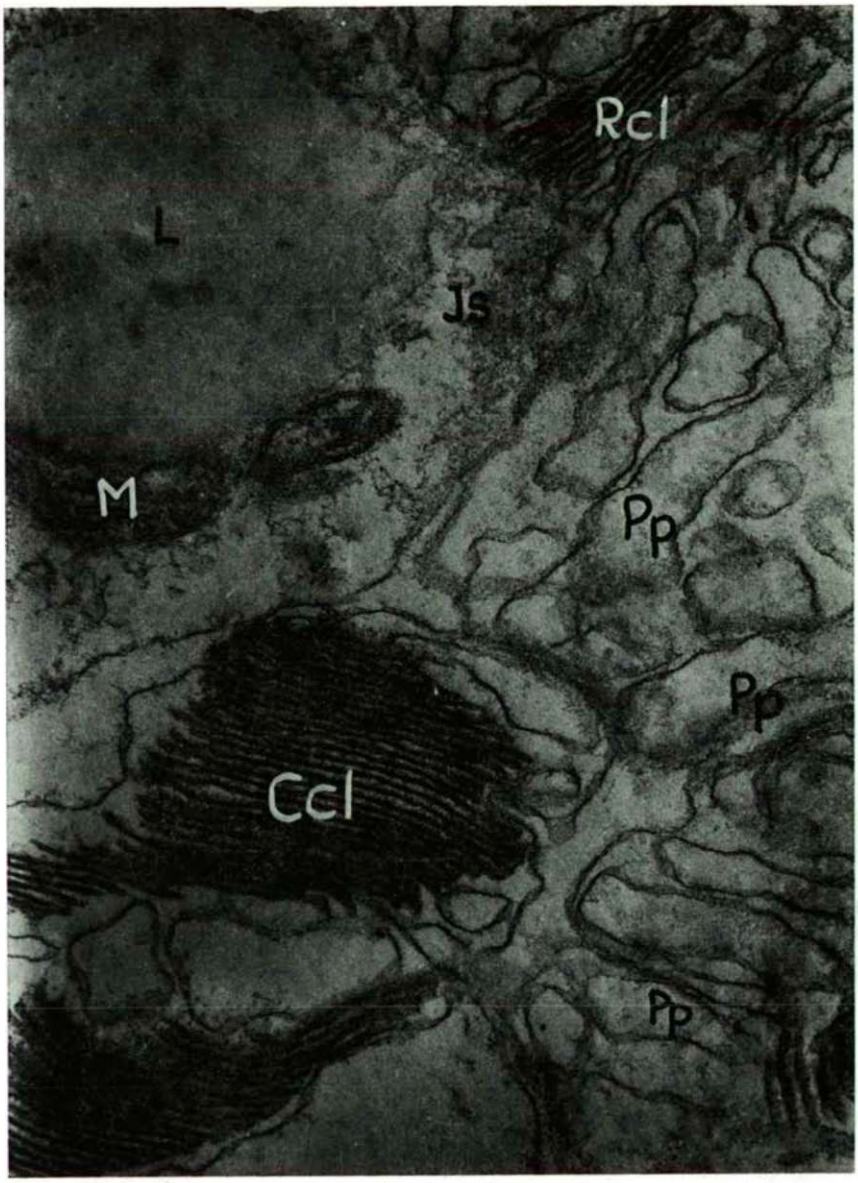

Fig. 1. Formation of the lamellar system of outer segment and of the inner segment of *Gallus domesticus* (6-day old). Rcl = rod-cell lamellae, Ccl = cone-cell lamellae, Is = inner segment, L = lipid droplet, M = mitochondrion, Pp = processes of pigment epithelia. Electron micrograph: x48 000.

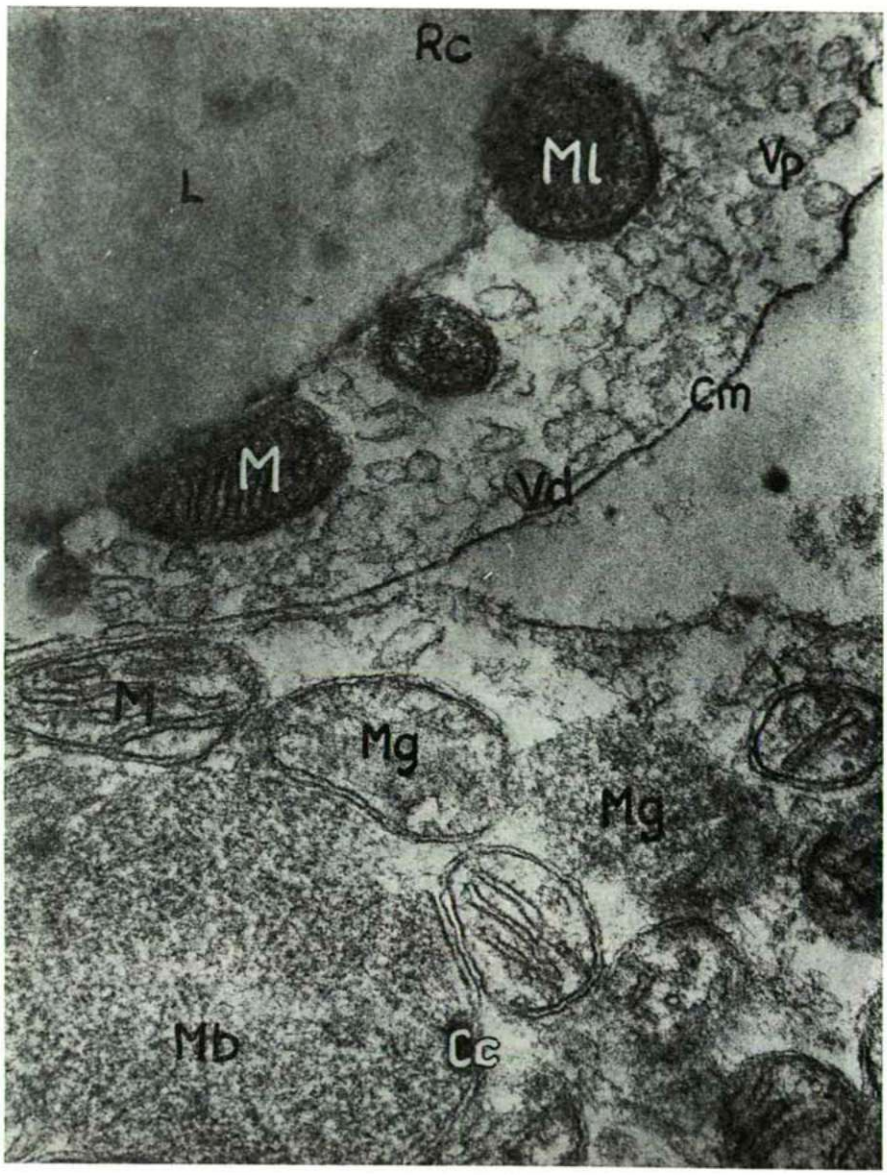

Fig. 2. Details of inner segments of the different types of visual cells of *Gallus domesticus* (8-day old). Rc = rod cell, Cc = cone-cell, L = lipid droplet, Mb = granulated central body, M = intact mitochondria, Ml = merging mitochondria undergoing granulation, Vp = cytoplasmic vesicle, Vd = vesicle for transmitting stimuli, (synaptic vesicle). Electron micrograph: x64 000.

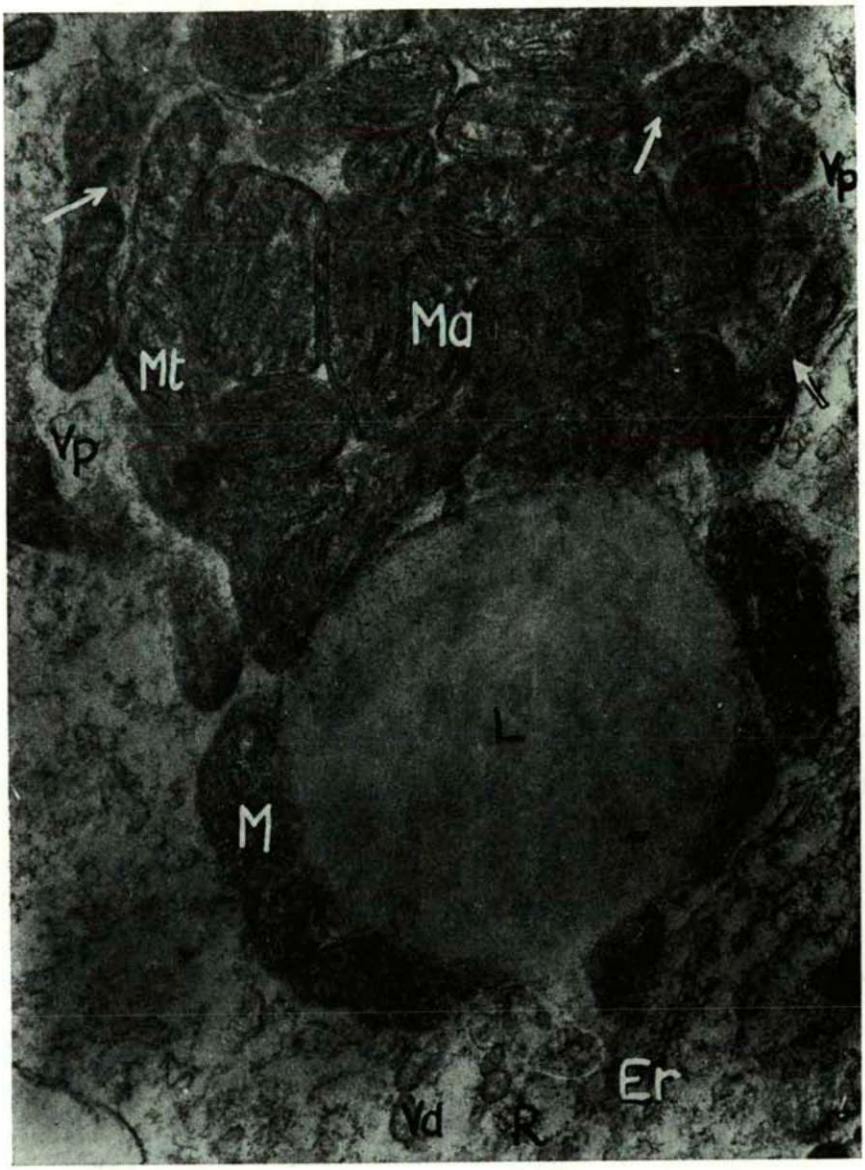

Fig. 3. Inner segment of a rod cell of *Gallus domesticus* (8-day old). L = lipid droplet, M = mitochondria, Ma = Aggregate of mitochondria, Mt = mitochondrial tubules, Er = rough endoplasmic reticulum, R = free ribosome, Vp = cytoplasmic vesicle, Vd = synaptic vesicle. (Arrows indicate constricted mitochondria.) Electron micrograph: x36 000.

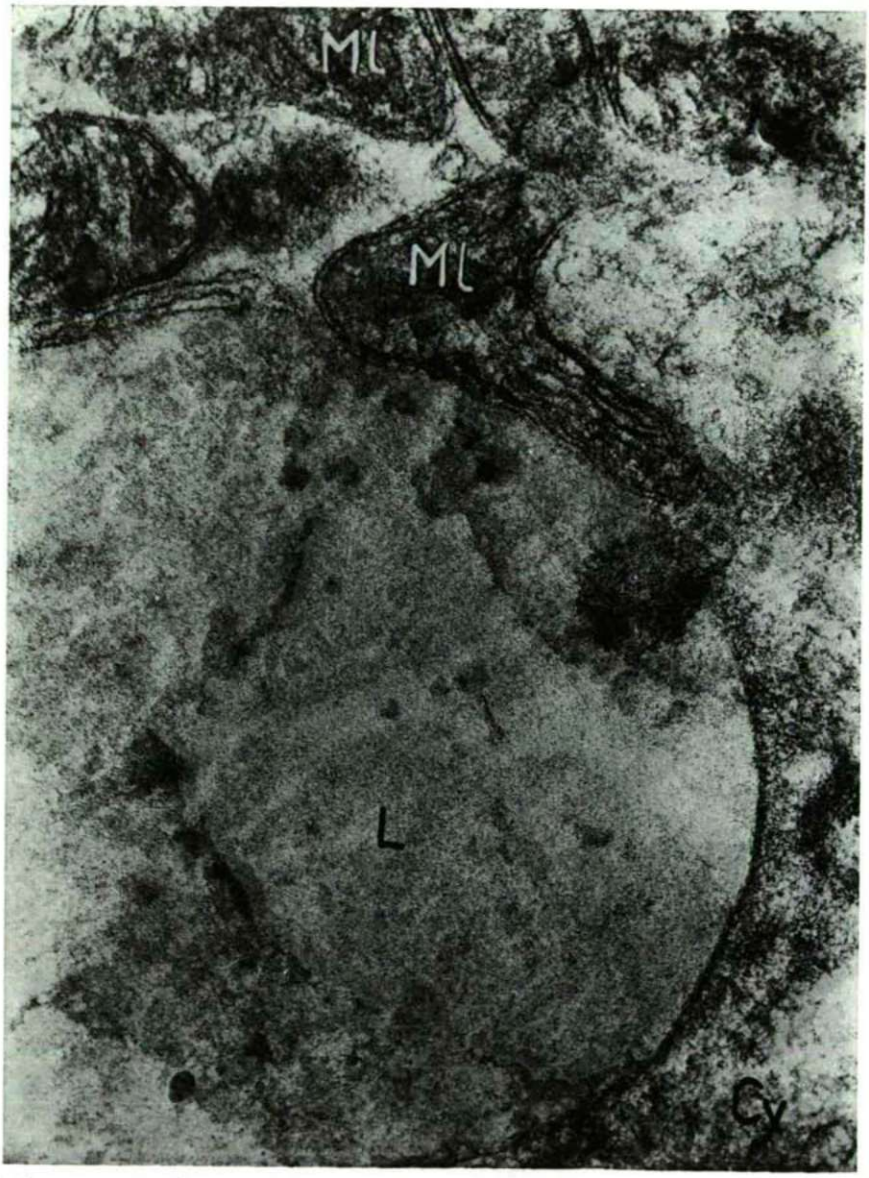

Fig. 4. Inner segment of a rod cell of *Gallus domesticus* (8-day old). Cy = cytoplasm, L = lipid droplet, Ml = mitochondrion merged into a lipid droplet. Electron micrograph: x64 000.

penetrates into the lipid droplet. Before the penetration, in the basic substance of mitochondria the decomposition of the tiny granules can be noticed, then the membrane opens and we may suppose that the contents run into the lipid droplet. The size of the lipid droplet can be increased permanently by the persumably very rapid metabolism and transport of materials, and it may also be observed in semi-thin sections that the lipid droplets are "spotted". The merging mitochondria are replaced by intact mitochondria migrating from the periphery to the lipid droplets. We have frequently seen constricted mitochondria among the grouping places indicated with an arrow (Fig. 3). Similar phenomena can never be observed in the older longish mitochondria or in the nuclear region.

Cone cell

In the cytoplasm of the inner segments, of the cells classed cone cells, there is no lipid droplet. There is a group of mitochondria, here also, situated towards the peripheral outer process, but they do not cohese. The mitochondria to be seen here are much more distinct. Their membrane consists of closed, double membranes, similar to the mitochondria of the rod cell, but the inner tubular structure is less. Gradual fusion of the cone cell mitochondria and the rearrangement of their lamellar systems maintain a centrally situated, strongly granulated "central body". The mitochondrial fusion can be seen particularly well in our Fig. 5. The granules of the central body migrate in part of the nuclear portion of the cone cell by cytoplasmic streaming but many more granules can be seen migrating towards the periphery and this suggest it is possible that play an important role in starting off the pigment production of the cells of the pigment epithelial cells.

Basal parts of the visual cells

The rod cell has, as is well known, a longish nucleus and a thin perikaryon. With its process of fairly thin (450 Å) diameter it penetrates deeply in the direction of the bipolar cells and gets in synaptic touch with its rod bipolar cell by means of its very small spherule. In the nuclear region of the rod cell a weakly developed endoplasmic reticulum is noticeable. Along the cisternae of the endoplasmic reticulum some ribosomes appear, and at the basal end irregular groups of these are also visible. Apart from the ribosomes there are round dark granules of small size (250 Å) and larger ones (380 Å). Some lighter "cytoplasmic vesicles" which are ovoid usually occurred. The darker vesicles run in the direction of the spherula they are, therefore, to be considered as synaptic vesicles. It is interesting that already in the vicinity of the nucleus a strong, dense membrane fragment appears (Fig. 6). This lathlike formation may aptly be named a "ribbon lath". Similar laths appear, but only much later, in the perikaryon of cone cells, mainly in the thick proximal process of this, forming its continuation, which, with its enlarged peduncle, shows a number of synaptic connections with the strongly ramifying dendrite ends of the cone bipolars (Fig. 7).

Discussion

The development of the young visual cells, sharply separated from one another and from the processes of the pigment epithelium, varies greatly in respect of the inner segment, at the beginning of the post-embryonic development. Among

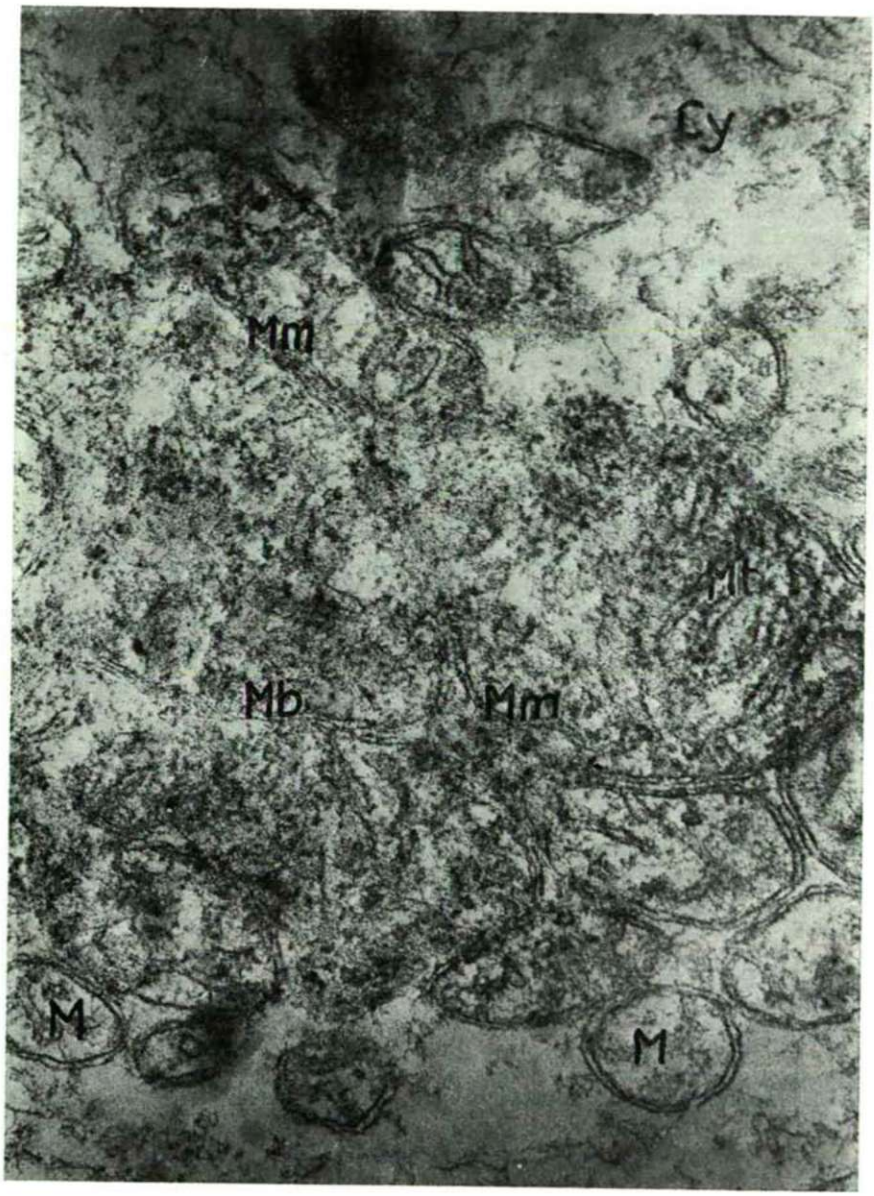

Fig. 5. Inner segment of a cone cell of Gallus domesticus (6-day old). Cy=cytoplasm, Mb=granulated central body, M=intact mitochondria, Mt=mitochondrial tubulus, Mm=mitochondrial membrane. Electron micrograph: x64 000.

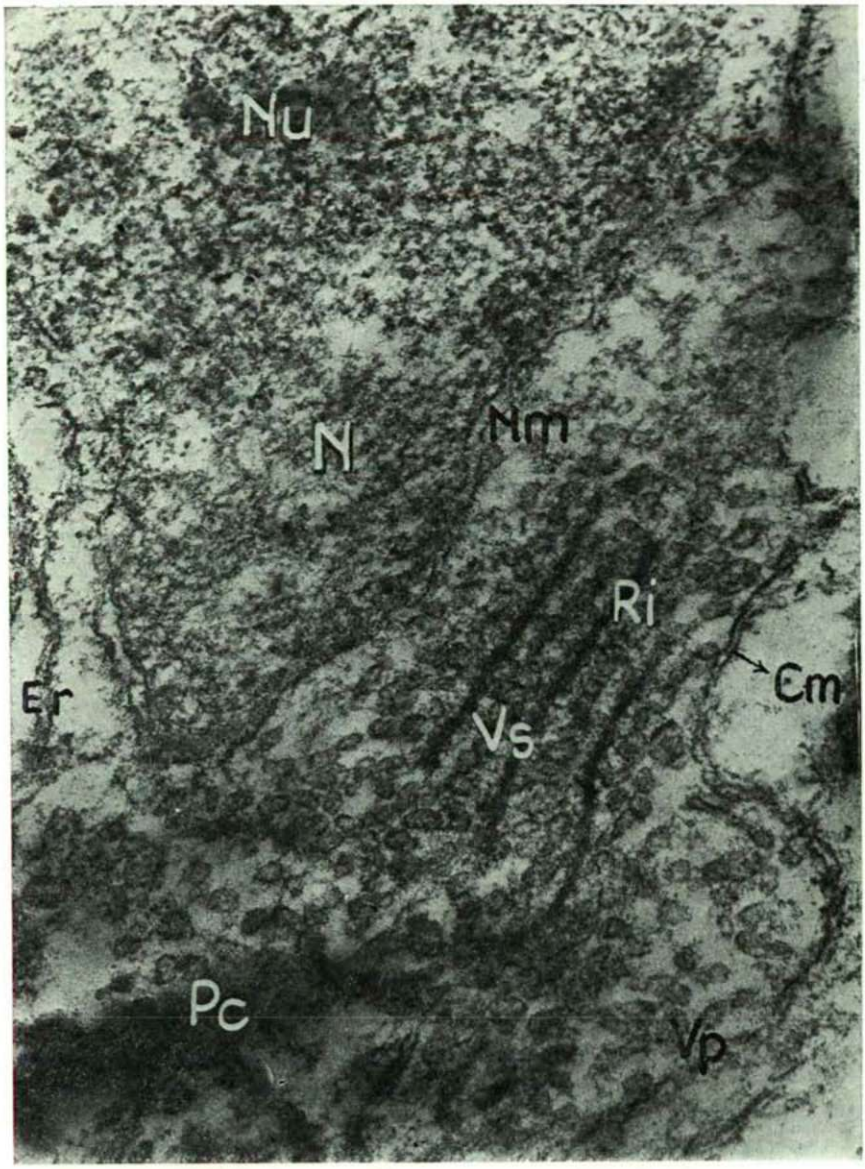

Fig. 6. Ending of the proximal central process (Pc), of a rod cell of *Gallus domesticus* (8-day old). Cm = cell membrane, N = cell nucleus, Nm = nuclear membrane, Nu = the separated chromatin of the nucleous, Er = endoplasmic reticulum, Vp = cytoplasmic vesicle, Vs = synaptic vesicle, Ri = ribbon precursors. Electron micrograph: x64 000.

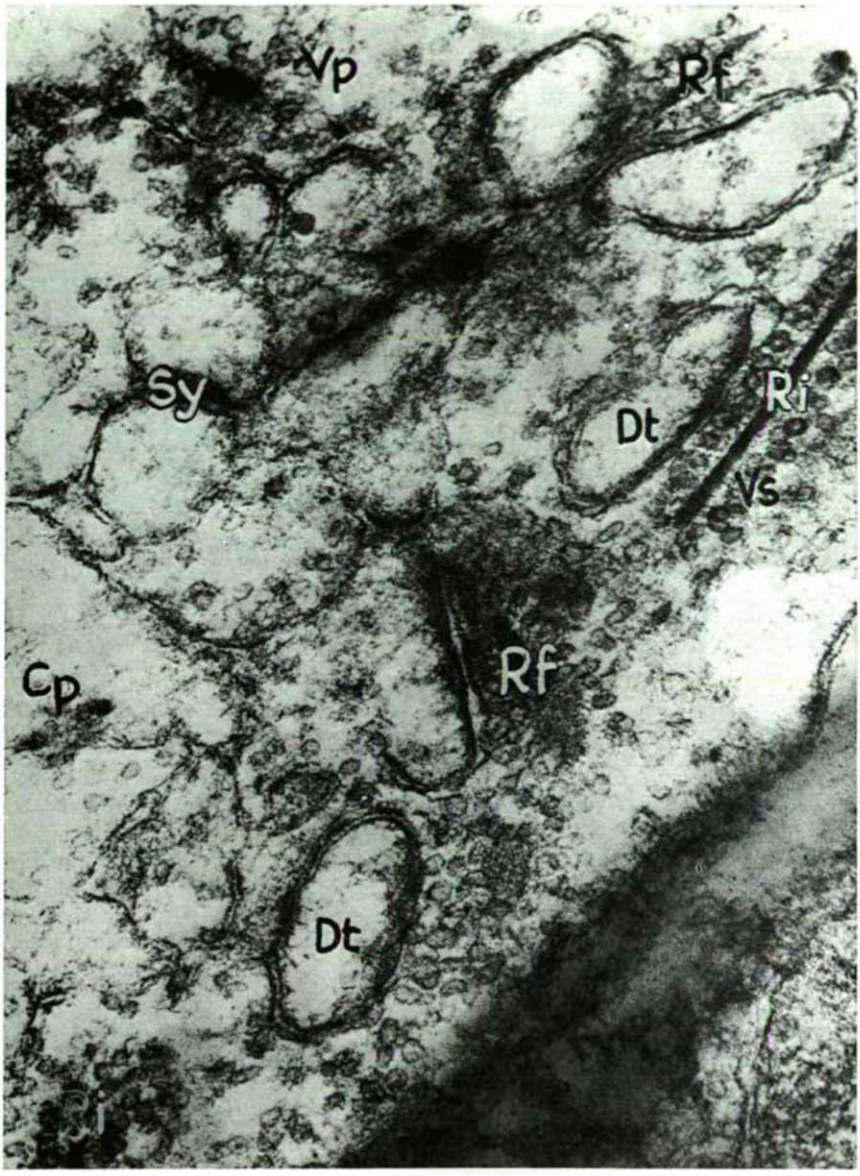

Fig. 7. Peduncle of the central process (Cp), of the cone cell of *Gallus domesticus* (20-day old) Ri = actual ribbon, Rf = ribbon in formation, Vs = synaptic vesicle, Vp = cytoplasmic vesicle, Dt = dendrite process, of bipolar, Sy = synapse. Electron micrograph: x64 000.

cytoplasmic organelles of rod cells, the mitochondria are connected with a lipid droplet of large size, merging gradually into that. The lipid droplet, indicating to the presence of some rhodopsine may persuate us to suppose that the rod cells may have a primary role in transmitting and transforming photons. The light stimulus is directed by two lateral ribbon lath at the proximal end.

In the inner segment of the rod cell there are also several mitochondria but of a different nature. The limiting membranes of mitochondria being decomposed, the central granulated body takes shape; its tiny granules primarily migrate towards the pigment epithelium and the result is possibly the inception of pigmentation. The granules can be discovered only later in the perikaryon of the cone cell, which is wider and rich in the usual cell organelles. Here apart from the cytoplasmic vesicles, a great number of slightly darker synaptic vesicles also appear. The investigation of these can be continued in the "ribbon synapses" between the peduncle of the cone cell in the retina of 20 days old chick (Fig. 7) and the cone bipolar cell forming rich penetration with their protrusions.

It may be supposed that during the transmission of the colour stimulus the ribbon systems, which lie in several directions, allow the "polarisation" of different colours in one direction. As seen in Fig. 7, it seems that the thickened synaptic membrane becomes the ribbon lath.

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