MORPHOLOGY AND PATHOMORPHOLOGY

INTERNEURANAL CONNECTIONS OF THE EXTERNAL GENICULATE BODY OF THE CAT

G. P. Obukhova

From the Laboratory of Morphology (Head – Corresponding Member of the Academy of Sciences of the USSR Prof. N. G. Kolosov) of the I. P. Pavlov Institute of Physiology (Director – Academician K. M. Bykov) of the Academy of Sciences of the USSR, Leningrad

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The question of interneuronal connections in the central nervous system has not been adequately studied in spite of a large number of investigations. This also applied perfectly to a number of problems relating to the conducting pathways in the central nervous system and to the study of the synaptic endings themselves. The study of the interconnection between the different divisions of the visual analysor has for a long time attracted the attention of research workers. There are many reports in the literature dealing with the structure of the external geniculate body and also with its connections with the peripheral part of the visual analysor – the retina – and with the visual area of the cortex.

The most complete investigations on the structure of the external geniculate body are those by Thuma [18], Rioch [16] and others. These workers showed that the external geniculate body consists of two nuclei – dorsal and ventral. In the process of phylogenesis the importance of the dorsal nucleus increases and in it terminates the bulk of the optic fibers. Depending on the species of animal, the dorsal nucleus consists of a varying number of cell strata. In respect of the ventral nucleus there is still no unanimity in the literature. On the question of whether optic fibers terminate in the ventral nucleus, the findings are contradictory. The connections of the external geniculate body with the retina have been studied both by the method of cell degeneration [3, 12, 13 and others] and by the method of degeneration of fibers. Minkowski [12, 13] showed that the direct and crossed optic fibers terminate in different strata of the dorsal nucleus. His observations, based on the method of transneuronal degeneration of cells, were subsequently confirmed by the findings of L. Ia. Pines and I. E. Prigonnikov [3]. On the basis of findings obtained by the use of Marchi's method of degeneration of fibers, the retina is projected in the external geniculate body as an inverted image. The direct and crossed fibers terminate in different parts of the dorsal nucleus.

With the problem of the place of termination of the direct and crossed fibers in the external geniculate body is directly connected that of the mode of termination of the optic fibers in this particular formation. Ramón-y--Cajal [15], using Golgi's method, found that the optic fibers terminate in the geniculate body of the cat in free racemose ramifications around the cells of the dorsal nucleus. Other workers [7, 8], using in their experiments on cats, rabbits and monkeys special methods for demonstrating synapses, showed that the fibers of the optic tract do not terminate in free endings; they form synaptic endings on the bodies and dendrites of cells. These authors studied the interneuronal connections of the external geniculate body of the cat in normal and experimental conditions and demonstrated the presence of synapses but made no attempt to relate these to the cell architecture of this formation. However, a more complete idea of the interneuronal connections may be obtained on the basis of comparison of the distribution of synapses in different portions of the external geniculate body with the cell architecture of this particular formation.

The object of the present investigation was to study the interneuronal connections of the external geniculate body of the cat in normal and experimental conditions and to compare the results obtained with the cell architecture of the external geniculate body.

EXPERIMENTAL METHOD

The material used in the investigation was the external geniculate bodies from normal cats and from cats after operation. In the experimental animals the optic nerves, chiasma and optic tracts were also investigated. The operation consisted of section of the optic nerve. The animals were killed on the 2nd, 3rd, 4th, 6th and 7th days after operation. The material was treated by the following methods: 1) Nissl's, 2) Ramón-y-Cajal's, after preliminary fixation for 24 hours in chloral hydrate, 3) the Golgi-Deinek method and 4) the Bielschowsky-Gros method. Sections were cut to a thickness of 20-25 μ.

In studying the experimental material the Golgi-Deinek and Bielschowsky-Gros methods were used.

EXPERIMENTAL RESULTS

Structure of the external geniculate body. On the basis of the study of a series of sections the cell structure of the external geniculate body of the cat may be represented as follows. The main mass of cells is the dorsal nucleus, which is present in all the sections, starting from the oral pole and ending at the caudal. The ventral nucleus appears only on certain sections near to the caudal pole and occupies only a small area in relation to the dorsal nucleus. During a study of a series of sections from the oral to the caudal pole, the dorsal nucleus is seen to be in three layers. According to the classification of Minkowski [13], these three layers are called the external peripheral layers, the internal peripheral layers and the central layers. In all these layers the presence of 3 types of cell – large, medium and small – may be observed. In the ventral nucleus are mainly to be found transitional forms from medium to small cells. Within the bounds of the dorsal nucleus, as the series is studied in a caudal direction, projection fibers may be observed in the dorsolateral aspect of approximately the middle third of the external geniculate body. Between these fibers are scattered large ganglion cells. In these same sections, dorsal to the bundle of projection fibers appears a small group of cells, which form an area of the dorsal nucleus separated from the main cell mass by the projection fibers. It must be pointed out that in the cat, at approximately the level of the oral division there is a reticular layer which surrounds the external geniculate body. In this layer are scattered nerve cells of medium size.

In the preparations of the external geniculate body of the normal cat, stained by the methods of Ramón-y--Cajal, Golgi-Deinek and Gros -Bielschowsky, it can be seen how the optic fibers enter the external geniculate body. The presence of terminal endings of characteristic appearance is seen on the body and dendrites of the cells of all the layers of the dorsal nucleus. As a rule these are loops or small rings, round or oval in shape. Sometimes synapses are met in the form of a special type of reticulum. In the majority of cases a connection is seen between the terminal ring or loop and the preterminal ramification of the fiber. In Fig. 1, a is illustrated a cell of the dorsal nucleus of the external geniculate body of the cat. As can be seen, the fine preterminal branches approach the cell and terminate on its body and dendrites in rings, loops or peculiar ring-like endings. In some cases synapses are also observed outside the connections with the preterminal fibers. In Fig. 1, b is shown a cell of the external geniculate body, situated between projection fibers.

Characteristically on these cells a comparatively large number of synaptic endings is almost always found. In Fig. 1, c is illustrated a cell with synaptic endings as revealed by the Bielschowsky-Gros method.

The number of synapses in our sections for one cell of the external geniculate body varies from 2 to 40; these variations are probably due to the fact that impregnation of the synapses depends on the their functional stage at the time of fixation. Synapses are distributed over the whole surface of the cell and its dendrites; they are particularly numerous at the point of emergency of the processes from the cell body. The diameter of the synapses on the cells of the external geniculate body varies from 2.5 to 3μ.

Degenerative changes in the external geniculate body of the cat after section of one optic nerve. Two days after section of one optic nerve, individual cells situated in the central layer of the dorsal nucleus of the ipsilateral external geniculate body show a slight increase in size,as compared with normal,of their argentophillic synapses (Fig. 2, a). However, in addition to these there are also some quite normal endings. In the opposite external geniculate body no altered synapses are to be found after 2 days. In studying the sections at this stage we were unable to find any destructive changes whatsoever in the optical fibers themselves.

On the 3rd day (see Fig. 2, b) after section of the optic nerve, degenerative changes are observed in the synapses on cells situated in the central layer of the ipsilateral external geniculate body, and also in the peripheral

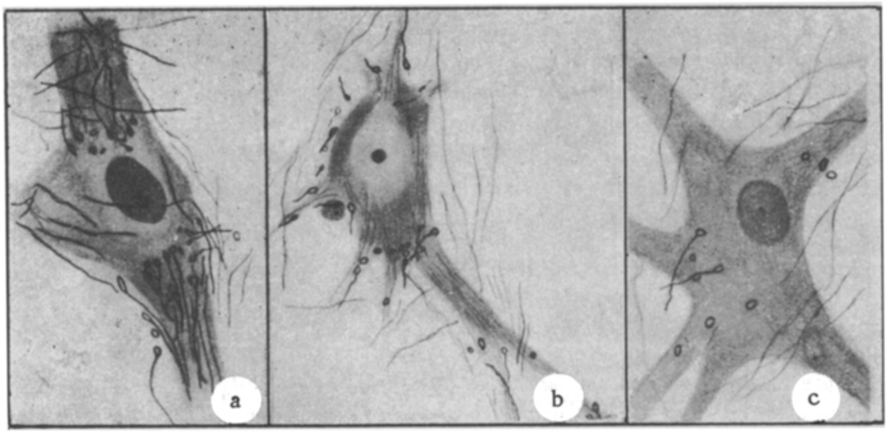

Fig. 1. Normal synaptic endings on the cells of the external geniculate body. a) On a cell of the dorsal nucleus. Ramón-y-Cajal's method. Objective 90, ocular 15; b) on a cell between the projection fibers. Golgi-Deinek method. Objective 90, ocular 15; c) on a cell of the dorsal nucleus. Bielschowsky-Gros method. Objective 90, ocular 15.

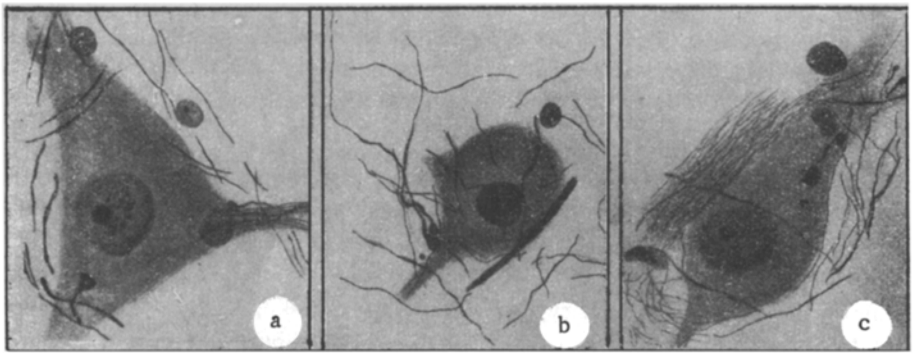

Fig. 2. Various stages of degeneration of synaptic endings on the cells of the dorsal nucleus.
a) Two days after section of the optic nerve. Bielschowsky-Gros method. Objective 90, ocular 15; b) 3 days after section of the optic nerve. Bielschowsky-Gros method. Objective 90, ocular 15; c) 4 days after section of the optic nerve. Bielschowsky-Gros method. Objective 90, ocular 15.

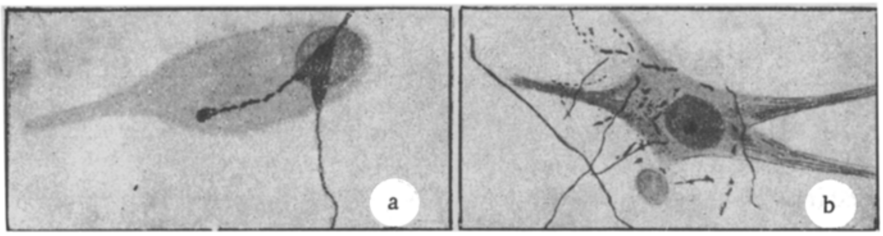

Fig. 3. Degenerating synaptic endings and fibers in the dorsal nucleus.
a) Four days after section of the optic nerve. Bielschowsky-Gros method. Objective 90, ocular 15; b) 6 days after section of the optic nerve. Bielschowsky-Gros method. Objective 90, ocular 15.

layers of the contralateral external geniculate body. Degeneration of the synapses is shown by a progressive enlargement of the synapses as compared with normal, and by their greater argentophilia. In some cases the cavity of the synapse is almost completely impreganated with silver. At this stage of degeneration the optic fibers have already undergone considerable alteration; their silver-staining properties are increased; they are slightly thickened as compared with normal, and a small proportion of the fibers in the ipsilateral external geniculate body have undergone partial fragmentation. In some sections it may be seen how one optic fiber divides into 3 or 4 branches. Synapses are also found lying in the intercellular space.

On the 4th and 6th days after section of the optic nerve terminal endings can be seen in all stages of degeneration. This fibrils are still present, terminating in normal synapses; however the majority of the terminal loops and rings are now converted into solidly stained bulbs with uneven contours, and within the individual endings the presence of fine granules is seen. In Fig. 2, c is illustrated a cell from the central layer of the dorsal nucleus of the ipsilateral external geniculate body, on which are seen both degenerating ending with a granular substance within, and normal rings. The size of the degenerating synapses greatly exceeds that of the normal synapses. At this stage completely fragmented synapses are observed on individual cells of the peripheral layer of the dorsal nucleus of the contralateral external geniculate body, and moreover the fragmentation extends as far as the preterminal fiber (Fig. 3, a). Furthermore the majority of the fibers entering the external geniculate body are undergoing severe fragmentation (see Fig. 3, b). Synapses are observed in different stages of degeneration, mainly on the medium-sized cells. A large number of degenerating synapses is also found on the cells of the reticular layer. In addition to these, normal synaptic endings may be observed on the large cells of both ipsi- and contralateral external geniculate bodies.

The entire picture of degeneration of synapses and fibers applies to cells and fibers situated in the central and peripheral layers of the external geniculate body on the operated and also on the opposite side. It should be mentioned that during the first 3 days after operation, degeneration was seen most sharply in the ipsilateral external geniculate body. In the ventral nucleus, neither in normal nor in experimental conditions was it possible to find any synaptic endings. In the same way we were unable to detect degeneration of synapses on the cells situated between the projection fibers.

The question of the interneuronal connections in the external geniculate body of the cat is mainly connected with the character of the endings of the optic fibers. Our findings in respect of the endings of the optic fibers in the external geniculate body of the normal cat, based on methods of demonstration of synapses, suggest that the opitc fibers form endings on the bodies and dendrites of the cells of the dorsal nucleus of the external geniculate body, shaped like loops, rings or reticula, splitting up into separate fibers. In addition synaptic endings are found on the cells lying between the projection fibers and on the cells of the reticular layer of the external geniculate body.

During examination of the shape of the normal synapses it was most usual to observe loops or rings of a round, oval or elongated shape. Sometimes synapses in the form of reticula were seen. Identical shapes of endings are also seen in other divisions of the central nervous system in mammals [1, 2, 5, 14, etc.] and man [11, etc.].

It was shown that a cell of the external geniculate body of the cat may have a large number of contacts with the optic fibers; in some cases up to 40 synapses may be observed on the body of the cell and its dendrites. In our sections it was not possible to estimate directly whether this number corresponds to one optic fiber or whether each fiber terminates in only one synapse, since on account of the thinness of the sections the preterminal branch could not be traced for a long way from the synapse. However, in some cases the initial division of the optic fiber may be seen at its point of departure from the tract; this suggests that one optic fiber has endings on several cells.

By comparing the findings on interneuronal connections with the cell architecture of the dorsal nucleus we found the presence of synapses in all the layers on large, medium and small cells. Synapses were discovered, too, on cells situated between the projection fibers and on the cells of the reticular layer.

In consequence of section of one optic nerve, we observed at different intervals of time after the operation degenerative changes in the synapses, mainly on middle-sized cells situated in the dorsal nucleus of the external geniculate body on both the side of operation and the oposite side. A similar pattern of degeneration was observed by Glees and Clark [8] and Glees [7] in the external geniculate body of the monkey and cat, and also by M. P. Frolova [4], Hoff [10], Gibson [9], Schimert [17], Auer [6] and others in various divisions of the central nervous system.

Comparison of the areas of degeneration with the cell architecture of the external geniculate body showed that after section of one optic nerve, degenerative changes are observed in synapses and fibers situated mainly in the central part of the ipselateral external geniculate body and in the peripheral parts of the contralateral external geniculate body. The presence of solitary normal synapses on the 6th day after operation, on the large cells of both external geniculate bodies and the absence of degenerative changes in the synapses on the cells between the projection fibers leads us to postulate that these endings belong to some other afferent system. These may also be the endings of afferent fibers leading, according to several workers, from the occipital lobe of the cortex to the external geniculate body, and finally, they may belong to local connections. This question cannot be considered to be finally settled.

From the investigations described the following conclusions may be drawn:

1. Synaptic endings are normally found on all 3 types of cell in the dorsal nucleus of the external geniculate body and also on cells situated between the projection fibers.

2. The number of synapses in contact with a cell body and its dendrites may reach 40.

3. After section of the optic nerve, at different intervals of time after operation degenerative changes are observed in synapses situated mainly on the medium-sized cells of the dorsal nucleus of both the ipsi- and contralateral external geniculate bodies. Degenerating synapses are found in large numbers on the cells of the reticular layer.

4. On the basis of the study of degeneration of synapses and fibers in the external geniculate body after section of the optic nerve, it may be supposed that the optic fibers not only terminate in the different parts of the dorsal nucleus, but are also to some extent connected with the reticular layer.

SUMMARY

The cytoarchitectonics and the interneuronic connections of the external geniculate body was studied in normal conditions as well as in section of the optic nerve. The synapses were revealed on the 3 types of cells of the dorsal nuclei and on the cells located between the projection fibers. After section of the optic nerve the degenerative changes were noted in the synapses and the fibers of various portions of the dorsal nucleus in the external geniculate body. These changes were revealed on both sides. Degenerating synapses were also found on the cells of reticular layer. It is assumed that the optic fibers terminate not only on the cells of the dorsal nucleus but are to a certain extent connected with the reticular layer.

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