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THE TERMINATION OF OPTIC NERVE FIBERS IN THE ALBINO MOUSE

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SYNOPSIS

To establish the terminal sites of the optic nerve fibers in the albino mouse, the immunohistochemical method using cholera toxin, subunit B (CTB), as well as three kinds of selective silver impregnation methods for degenerating nerve fibers were used. Termination was confirmed in the following nuclei: bilateral dorsal nuclei of the lateral geniculate body (LGB), ventral nuclei of LGB, preoptic areas, posterolateral nuclei, superior colliculi, suprachiasmatic nuclei, medial terminal nuclei of the accessory optic tract (AOT), and dorsal terminal nuclei of AOT. The percentage of the optic nerve fibers crossing at the optic chiasm was estimated at 90 to 95. Fibers from the unilateral retina were observed to terminate more in the contralateral nucleus. With regard to the suprachiasmatic nucleus, however, the terminations were observed to be distributed evenly and bilaterally.

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INTRODUCTION

Many studies on the termination of optic nerve fibers in mammals have been carried out this century. Most of them were performed on rat while studies of the mouse are rather limited. These studies were carried out by Colman et al.[2], De Renzi et al.[3], Draeger[4,7], Draeger and Hubel[5], Draeger and Olson[6], Gillilan[10], Grafstein[11], Grafstein and Laurento[12], Gurjian,[13] Iwahori et al.[16], Wenisch[28], Yamada[30], and Youngstrom and Nunez[33]. Various methods, such as selective silver impregnation for degenerating axons[25], horseradish peroxidase[14], tritiated amino acids[17], and electron microscope[28] were used for tracing or detection of the degenerating axons and their terminals. To determine any possible divergence of optic nerve fiber termination from albino rat, we examined the terminals in the albino mouse using selective silver impregnation methods, but were unable to obtain significant results particularly on terminal sites in the hypothalamic areas as well as on the accessory optic nuclei. Therefore, to establish the terminal sites of optic nerve fibers in these areas, we repeated the study using the immunohistochemical method of Cholera toxin, subtype B (CTB), which has been used[1,20,21,26] to elucidate the termination of a limited number of nerve fibers.

MATERIALS AND METHODS

Fifteen albino mice of dd-strain weighing 20 to 30 g were used. In 5 mice the right eyeball was enucleated by cutting the optic nerve at its origin. The animals were sacrificed under deep ether anesthesia on the 5th, 7th, 10th, 16th and 20th days after enucleation by transcardial perfusion of 10 % buffered formalin from the left ventricle and then the brain was removed and immersed in the same fixative for more than 10 days. After being embedded in gelatin, the brain was frozen and serial sections of 25 μm thickness were prepared using a cryostat. Thereafter, the sections were stained either with Nauta-Gygax[22] or Fink- Heimer[9] method for degenerating nerve fibers. In another group of 5 mice, the right eyeball was enucleated by the same method and these animals were sacrificed 5 days after enucleation by transcardial perfusion of a 10 % buffered formalin. The brains were cut serially at 25 μm thickness by cryostat and the sections stained using Yamadori's[31] selective silver impregnation method for degenerating axons. The main procedures of this method were as follows:

1) Transfer sections to 0.05 % potassium permanganate and agitate intermittently for 5 to 15 minitues.
2) Transfer sections to 1:1 solution of 1 % oxalic acid and 1 % hydroquinone and agitate until completely decolorized.
3) Soak sections in 0.3 or 0.5 % phosphomolybdic acid for 5 to 10 minutes.
4) Wash sections thoroughly in at least 3 dishes of distilled water before 1) and after 1),2),3).
5) Transfer sections to freshly made ammoniacal silver nitrate solution (100 ml 1.5 % silver nitrate, 50 ml absolute ethanol, 10 ml strong ammonia water, 8 ml 2.5% sodium hydroxide) and agitate for 2 to 10 minutes.(Ammonia water was indicated as ammonium hydroxide in the original papaer.)
6) Transfer sections to Nauta-Gygax's reducing fluid and agitate vigorously for about 1 minute.
7) Wash sections in distilled water and soak them briefly in 1% sodium thiosulfate.

In the remaining 5 mice, subunit B of Cholera toxin (CTB) was injected intraocularly to label the entire retinofugal optic nerve fibers anterogradely. Animals were anesthetized using

ether. Then, 10 μl of 0.05 % CTB was injected into the vitreous body. After 5 days of survival for axonal transport, the animal was sacrificed by transcardial perfusion of a mixed solution of 4 % paraformaldehyde and 0.2 % picric acid in 0.1 M phosphate buffer solution (PBS) (pH 7.6). The brain was removed from the skull and postfixed overnight in the same fixative at 4 °C and cryoprotective soaking in a 20 % sucrose solution in PBS was performed for 24 hours. Finally the brain was sectioned at 25 μm thickness using a cryostat.

The immunohistochemical detection of CTB was performed according to the following procedure:

1) Washing sections for 3 × 2 minutes in PBS to remove the remaining sucrose
2) Incubating sections in goat anti-CTB diluted 1 : 5000 in PBS containing Triton X-100, for more than 48 hours at 4 °C
3) Incubating sections overnight in biotinated rabbit antigoat antiserum diluted 1 : 1000 in PBS
4) Rinsing sections for 3 × 2 min in 0.1 M PBS after 2) and 3) procedures
5) Incubating sections overnight in a mixture of 1/1000 A + 1/1000 B solution of ABC kit of Funakoshi Co.
6) Rinsing sections for 2 × 2 min in 0.1 M PBS (pH 7.6)
7) Incubating sections in 20 mg diaminobenzidine dissolved in 100 ml Tris-HCl buffer for 2 hours at room temperature
8) Transforming sections into a 0.03 % H_2O_2/DAB solution for 5 to 10 min until the reaction becomes optimum
9) Transforming sections into 0.05 M Tris buffer solution (pH 7.5)
10) Mounting sections onto gelatinated glass slides

RESULTS

1. *The optic nerve fibers*

In mice sacrificed on the 5th day after operation, degenerating optic nerve fibers from the right retina were seen only ipsilaterally in the optic nerve and mainly contralaterally in the optic tract. Only a very limited number of degenerating fibers were seen on the ipsilateral optic tract. The crossing fibers form small fasciculi and these fasciculi from both sides intersect at the chiasm (Fig. 1-A).

In the preparations of the CTB-immunohistochemistry, CTB-labelled axons were seen as dark brown to black in color. By microscopic observation the ipsilateral optic nerve was seen as a dark brown bundle but the contralateral optic nerve was seen as colorless. The crossing fibers at the chiasm were seen as transverse dark brown layers or fasciculi, which was exactly the same pattern as had been seen in the silver impregnated sections. The rate of crossing of optic nerve fibers was presumed to be 90 to 95 percent.

2. *The ventral nucleus of the lateral geniculate body*

By observation of silver impregnated preparations, many degenerating optic nerve fibers and their terminals were seen only in the lateral division of this nucleus, particularly on the contralateral side. These fibers and terminals were not evident on the ipsilateral side.

In the lateral division of the contralateral ventral nucleus of the lateral geniculate body, the degenerating axons and their terminals were evident altogether as 3 dark brown striae running between the anterolateral and the posteromedial portions in the horizontal sections of the immunohistochemistry using CTB. The innermost striatum was seen only in the posterior half of the division. Two non-stained colorless striae as well as the lightly stained outermost optic fiber layer which contains transversely sectioned optic nerve fiber were evident among these dark

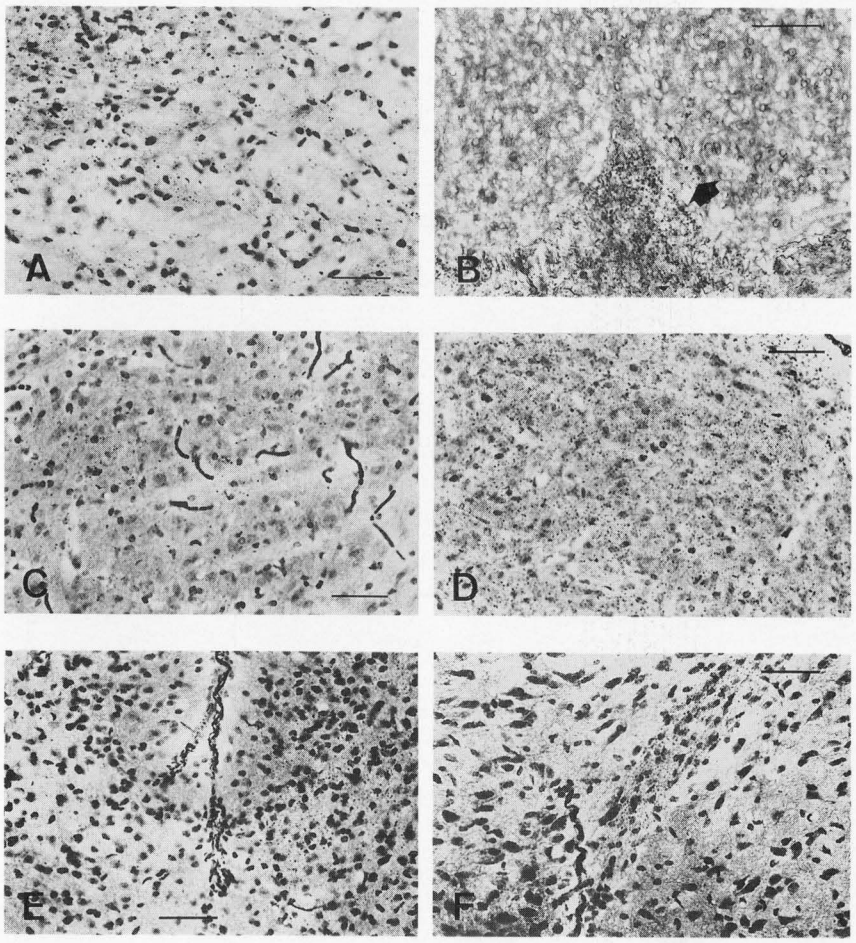

Figure 1. Photomicrographs of optic nerve fibers and their terminals by Yamadori's selected silver impregnation for degenerating axons except "B" which was stained with Nauta-Gygax's method. A: Optic chiasm, frontal section, B: Optic chiasm and suprachiasmatic nuclei, frontal section. Degenerating terminals in the nucleus are shown by an arrow. C: Ipsilateral dorsal nucleus of the lateral geniculate body (LGB), frontal section, D: Contralateral dorsal nucleus of LGB, frontal section, E: Medial portion of the superior colliculus (SC), frontal section, F: Contralateral medial terminal nucleus of the accessory optic tract (AOT), frontal section, Bar: 50 μ m

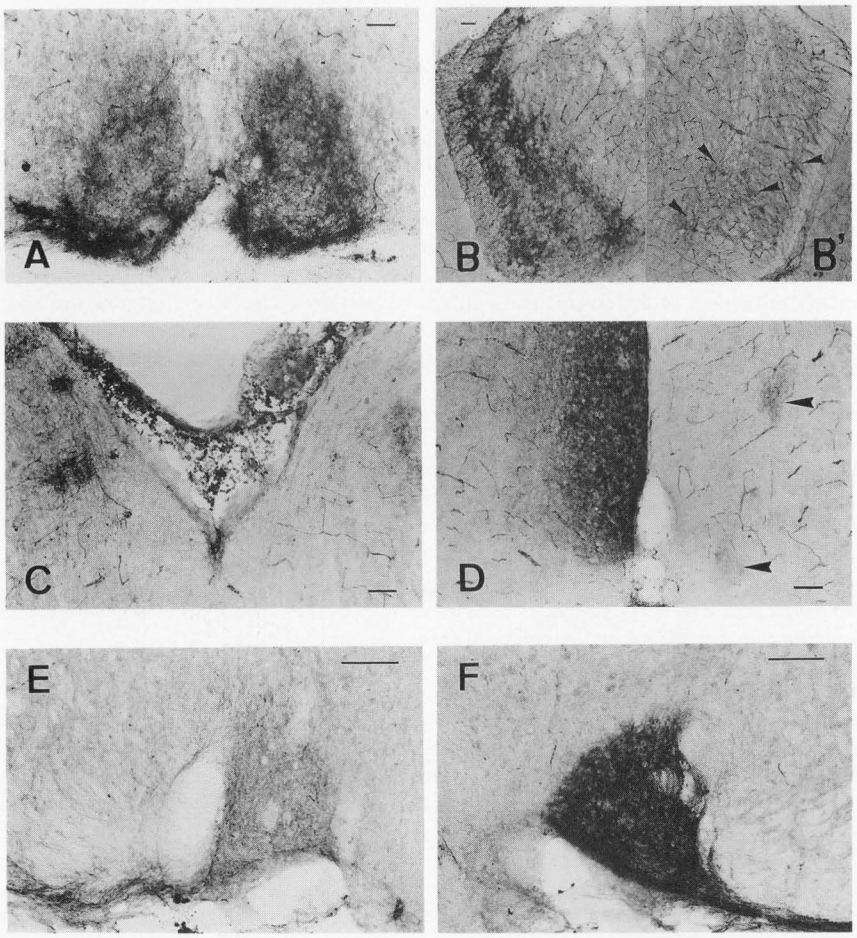

Figure 2. Photomicrographs of optic nerve fiber terminals by CTB immunohistochemistry, A: Bilateral suprachiasmatic nuclei, frontal section, B: Contralateral ventral nucleus of LGB, B': Ipsilateral ventral nucleus of LGB, Immunoreactive patches are indicated by arrow heads, horizontal section, C: Bilateral medial portions of the pretectal area, horizontal section, D: Bilateral medial portions of SC, horizontal section, E: Ipsilateral medial terminal nucleus of AOT, frontal section, F: Contralateral medial terminal nucleus of AOT, frontal section, Bar: 50 μ m

brown striae (Fig. 2-B). A few dark patchy areas corresponding to these striae of the contralateral nucleus were also observable in the same nucleus on the ipsilateral side (Fig. 2-B').

3. *The dorsal nucleus of the lateral geniculate body*

The degenerating axons and their terminals were seen as darkly stained dotted fibers or patches throughout the nucleus in the frontal sections of the silver impregnated preparations (Fig. 1-D). However, they were less densely distributed in the area dorsomedial to the central part of the nucleus on the contralateral side. In accordance with this finding, degenerating fibers and terminals were seen only in the dorsomedial to central part of the nucleus on the ipsilateral side (Fig. 1-C). This pattern of distribution was particularly evident in the anterior half of the nucleus.

In the contralateral nucleus, the immunohistochemically positive area of dark brown color was seen all over the nucleus in the frontal and horizontal sections but this darkly stained area was particularly prominent in the dorsolateral and ventral portions. The central portion was stained rather lightly. Observation of the horizontal sections revealed this lightly stained area spreading from the anteromedial to the central part of the nucleus. On the ipsilateral side, the darkly stained area extended from the dorsal anteromedial to medial to posteromedial part of the nucleus corresponding roughly to the lightly stained area on the contralateral side.

4. *The posterolateral nucleus (The posterior part of the lateral thalamic nucleus)*

On the contralateral side many dotted line-like degenerating fibers running between the ventrolateral and dorsomedial portions of the nucleus were observable in the silver impregnated sections. However, the number of dark dots which were thought to be terminals was limited. On the ipsilateral side, these fibers were scarcely observable. In the sections of CTB immunohistochemistry, a few patchy, densely stained areas were observable, but these areas were not recognized in the nucleus on the ipsilateral side.

5. *The pretectal area*

In the silver impregnated preparations, many degenerating fibers and terminals were seen in the medial optic tract nucleus or pretectal olivary nucleus on the contralateral side. Degenerating axons were particularly prominent in the area surrounding the nucleus. These degenerating fibers and terminals were observable in the whole area of the pretectum on the contralateral side. However, they were rarely seen on the ipsilateral side.

In the sections of CTB immunohistochemistry, the medial optic tract nucleus or pretectal olivary nucleus was seen as densely stained round structure in the frontal as well as in the horizontal sections. Small densely stained patches were also seen in the dorsal and dorsolateral parts to the nucleus. The other portions of the pretectal area were not so densely stained though they were slightly darker than the surrounding areas on the contralateral side. On the ipsilateral side, a darkly stained area was seen only around the medial optic tract nucleus (Fig. 2-C).

6. *The superior colliculus*

In the silver impregnated preparations, a large number of degenerating nerve fibers and their terminals were seen in this structure on the contralateral side, particularly in the optic and superficial gray strata. The degeneration was also observable in the intermediate gray stratum. The zonal stratum could not be differentiated from the superficial optic stratum in the mouse. A patchy group of degenerating axons were observable in the medial portion of the ipsilateral optic stratum. The degenerating terminals, however, were very limited in number in the superficial gray stratum or in the intermediate gray stratum. (Fig 1-E)

A dense immunohistochemical reaction product was seen throughout the superficial gray stratum of the contralateral colliculus by the observation of CTB immunohistochemical preparations. The optic and intermediate gray strata were lightly stained. On the ipsilateral side,

the area of reaction was recognized only in the medial or medial to posterior area of the optic stratum or in a part of the superficial gray stratum, where a few dark, small patchy areas were observable. (Fig. 2-D)

7. *The suprachiasmatic nucleus*

A very limited number of degenerating fibers seemed to enter the medial portion of the contralateral as well as ipsilateral suprachiasmatic nucleus by precise observation of the silver impregnated preparations. However, it was difficult to decide whether the fibers actually terminated in this nucleus or not, as the sections of positive finding were few. (Fig. 1-B)

On the other hand, a strong reaction of immunohistochemistry was found in this nucleus bilaterally by the CTB preparations. Among 5 cases of CTB immunohistochemical preparations, the reaction on the contralateral side was slightly stronger than that on the ipsilateral side in 3 cases, but the density was almost the same in another 2 cases. The peripheral portion of the nucleus was more dense than in the central in all 5 cases examined. (Fig. 2-A)

8. *The supraoptic nucleus*

No affirmative finding of the existence of optic nerve fiber terminals in this nucleus was obtained by the silver impregnation method used in the present study. Although it was not so evident as in the suprachiasmatic nucleus, the brownish color of reaction was stronger in this nucleus than in the surrounding hypothalamic structures in the preparation of CTB immunohistochemistry. The reaction products seemed more in the contralateral nucleus than in the ipsilateral one.

9. *The accessory optic system*

The degenerating optic nerve fibers as well as their terminals were seen clearly in the medial terminal nucleus and the anterior fasciculus of the accessory optic tract in the silver impregnated preparations; namely, fine dark silver granules were seen in the whole nucleus and the fasciculus (Fig. 1-F). Although the number of these degenerating fibers and terminals was limited, they were also seen in the dorsal terminal nucleus and its fasciculus on the contralateral side. On the ipsilateral side, however, these degenerating granules were not recognized in the dorsal terminal nucleus as well as in the area where the lateral terminal nucleus is thought to be located.

The medial terminal nucleus as well as the anterior fasciculus of the accessory optic tract showed very strong reaction of CTB immunohistochemistry, particularly on the contralateral side (Fig. 2-F). This reaction was also seen in the dorsal terminal nucleus and its fasciculus on the contralateral side. Although the reaction was rather weak in these structures on the ipsilateral side, it was clear that the optic fibers terminate in these accessory optic nuclei on the ipsilateral side (Fig. 2-E).

DISCUSSION

We used 3 kinds of silver impregnation method; namely, Nauta-Gygax[22], Fink-Heimer[9], and Yamadori[31] for selective impregnation of degenerating axons and terminals, and Yamadori's method[31] was thought to be the most favorable. As good results were obtained by preparations of 5 day survival samples as far as Nauta-Gygax[22] and Fink-Heimer[9] methods were concerned, the survival period was fixed as 5 days in Yamadori's method[31]. Nevertheless, there is a disadvantage in the silver impregnation method in general; namely, the degree of impregnation is different in each part of the optic projection as degeneration varies with axon diameter and the distance from the injury, even though the optimum survival time to discover degenerating terminals had been

fixed as 5 days. For this reason, it was difficult to identify terminals particularly in small nuclei or the area supplied with a limited number of optic fibers. To compensate for this shortcoming in the silver impregnation method, we used the immunohistochemical method of CTB for the anterograde tracing of optic nerve fibers, although to detect the limited number of projection was considered difficult even by this method. It was originally introduced by Stoeckel et al.[27] as a method of retrograde labeling of axons and used as neuronal labeling in tissue culture by Okada et al.[23] or for tracing fiber connections by Luppi et al.[18),19)], and Ericson and Blomqvist[8]. Wild[29] used Cholera toxin conjugated horseradish peroxidase (CT-HRP) as anterograde and retrograde labeling of nerve fibers projecting from the pretectal nucleus to the principal optic nuclei[26]. Shen and Semba[26] as well as Angelocci et al.[1] applied the method as an anterograde axonal tracing and reported its high sensitivity. As established by these authors, it was considered that this method was preferable for the present study. Nevertheless, this CTB immunohistochemistry still has a drawback in that the result is always dependant on the degree of antigen-antibody reaction and it is extremely difficult to establish the terminals of a small number. However, we found this method highly sensitive in revealing almost all of the optic nerve terminals.

The main terminal nuclei or structures of the optic nerve fibers in the albino mouse are thought to be almost the same as in the albino rat revealed by the silver impregnation[32]; namely, bilateral ventral and dorsal nuclei of LGBs, posterior part of the lateral thalamic nuclei, nuclei of the pretectal areas, superior colliculi, medial teminal nuclei of AOT, and the contralateral dorsal terminal nucleus of AOT. In addition to these structures, the bilateral suprachiasmatic nuclei and the ipsilateral dorsal terminal nucleus of AOT were established as terminals of the optic fibers in the albino mouse by observation of the CTB immunohistochemical preparations.

In the dorsal nucleus of the lateral geniculate body, the crossed optic nerve fibers seemed to terminate in the whole part of the nucleus except the area dorsomedial to the central part in the frontal sections. Meanwhile the non-crossing fibers concentrated in this area in the ipsilateral nucleus. It is an interesting finding that CTB immunohistochemistry positive reaction was recognized in 3 layers in the contralateral ventral nucleus of the lateral geniculate body. There is a possibility that the innermost layer belongs to the medial division of the nucleus. The reaction was not necessarily comparable with that of the ipsilateral side but a few patchy areas of reaction corresponding to these striae on the contralateral side were observable.

As for the suprachiasmatic nucleus, the optic nerve terminals could not be confirmed only by silver impregnation. Using immunohistochemistry, this nucleus showed very dense reaction products bilaterally not only in the albino mouse but also in the albino rat (not reported yet). Although we were unable to confirm the situation exactly, there is a possibility that each nucleus is supplied with the same number of optic nerve fibers in the albino mouse.

Contrary to the suprachiasmatic nucleus the obvious result of optic nerve fiber termination was not obtained in the supraoptic nucleus, not only by the observation of the silver impregnated preparations but also by the CTB immunohistochemistry. In this nucleus the density of the CTB immunohistochemical reaction was not so evident even in the contralateral nucleus as in the suprachiasmatic nucleus, though the brownish tone was denser in the nucleus than in the neighboring hypothalamic tissues including the ipsilateral optic tract. Therefore, the termination of optic nerve fibers could not be confirmed, though we were of the opinion that this was highly possible, particularly on the contralateral side.

By observation of silver impregnated preparations, we were unable to confirm any degenerating nerve fibers and terminals in the accessory optic fasciculi and their nuclei on the ipsilateral side except the medial terminal nucleus. However, the preparation of the CTB-immunohistochemistry showed the positive reaction of optic nerve fibers in these structures even on the ipsilateral side. The reaction of the lateral terminal nucleus, delineated by Hayhow et al.[15] in the rat, was not so strong as to indicate optic nerve termination. Therefore, we conclude that the

optic nerve fibers project bilaterally to the medial and dorsal terminal nuclei.

Recently Qu et al.[24] reported the existence of direct retinal projection to the contralateral lateral habenular nucleus in the rat. They confirmed these fibers by retrograde fluorescent labeling using Fluoro-Gold, Fluoro-Ruby or 4-acetamide, 4'-isothiocyanostilbene-2, 2'- disulfonic acid (SITS) as well as by silver impregnation. We looked for this projection in the albino mouse in our present study, but were unable to obtain a positive result.

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