Electrophysiological study of the posterior accessory optic tract[1]

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HAMASAKI, DUCO AND ELWIN MARG. *Electrophysiological study of the posterior accessory optic tract.* Am. J. Physiol. 199(3): 522–528. 1960.—Electrophysiological methods were used to detect the presence of the posterior accessory optic tract—transpeduncular tract in the rabbit. Photic stimulation gave rise to mainly an 'on' response from the contralateral nucleus of the transpeduncular tract. Electrical stimulation of the optic nerve fibers evoked a response from this nucleus with a latency of 1–3 msec. A response could not be elicited from the nucleus of the transpeduncular tract, the lateral geniculate nucleus, or the superior colliculus by ipsilateral stimulation. Encéphale isolé preparations showed that the responses recorded under urethane anesthesia were not altered by the drug. The nucleus of the posterior accessory optic tract is situated between the optic nerve and the nucleus of the transpeduncular tract, and lies on the dorsolateral aspect of the midbrain between the superior colliculus and the medial geniculate nucleus. No centrifugal fiber responses have been found which originate from the nucleus of the transpeduncular tract and pass to the retina via the optic nerve.

IN ADDITION to the main optic tracts leading from the mammalian eyes to the lateral geniculate nuclei, two pairs of accessory optic tracts have been reported in many animals including man (1). The most recent and thorough anatomical investigation of the accessory optic tracts appeared in 1941 (2); a systematic physiological investigation has never been made to our knowledge.

The purpose of this investigation is to verify by electrophysiological methods the presence of one of these accessory optic tracts, the transpeduncular tract, which has also been called the posterior accessory optic tract. In addition to determining the physiological properties of this pathway, we have attempted to clarify the findings of the anatomists as well as to resolve some of their disagreements. A preliminary report of this investigation has appeared earlier (3).

METHODS

A total of 35 rabbits was used. Thirty-three were under urethane anesthesia and two were encéphale isolé preparations. Cannulas were inserted into the trachea and one femoral vein. The animal was placed in the Horsley-Clark stereotaxic instrument and stereotaxic maps of the rabbit's brain (4) were used to locate the various structures in the midbrain.

Entomological needles were used to make the electrodes. They were completely insulated with a plastic coating except for a microscopic portion of the tip. The resistance of the electrode, in 0.9% saline solution, varied from 20,000 to 50,000 ohms (measured with a Simpson meter, model 260). The diameter of the insulated needle was 0.35 mm. The separation of the two needles of one electrode was varied from 0.5 to 1.5 mm.

The responses were fed to two direct-coupled amplifiers and were displayed on a dual-beam cathode-ray oscilloscope. A loud speaker was used to monitor the potentials.

Electrical stimulation was provided by two Grass stimulators through stimulus isolation units. Photic stimulation was provided by a beam of light focused in the plane of the pupil with an illuminance there of 220 foot candles. A small mirror reflected a part of the beam onto a photocell, the response of which indicated when the eye was being stimulated.

The temperature of the rabbit was monitored with a thermistor probe in the rectal cavity. A 6-v., d.c. heating pad was used to warm the animal when necessary.

One electrode was inserted into either the left optic nerve or the chiasma. The presence of an 'on-off' light response from this electrode indicated its location in the optic pathway, whereupon it was connected to the output of the stimulator. Pulses of suitable frequency, duration and strength were then delivered to the optic fibers.

The second electrode, which was aimed for the right nucleus of the transpeduncular tract, was set at Horsley-Clark co-ordinates $P = 7.5$, $R = 2.5$. A response was first seen between $H = +3$ to $+1$. This response has been found to arise from the optic fibers which make up the brachium of the superior colliculus. The response constituted evidence that the electrode in the optic nerve was stimulating optic fibers. The strength and polarity of the stimulus were adjusted to give a maximal response.

The response from the nucleus of the transpeduncular tract was observed between $H = -3$ to -4

Received for publication February 8, 1960.
[1] This investigation was supported by Grant G-6195 from the National Science Foundation.

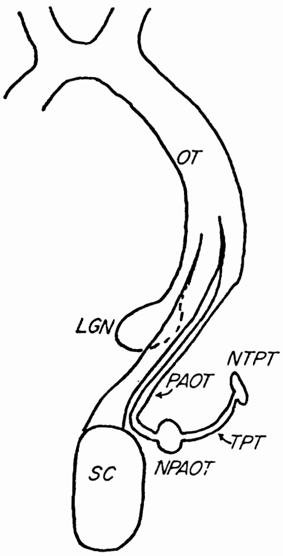

FIG. 1. Schematic diagram of the posterior accessory optic tract—transpeduncular tract. *OT*—optic tract; *LGN*—lateral geniculate nucleus; *SC*—superior colliculus; *PAOT*—posterior accessory optic tract; *NPAOT*—nucleus of the posterior accessory optic tract; *TPT*—transpeduncular tract; *NTPT*—nucleus of the transpeduncular tract.

At the end of an experiment, a small amount of iron was deposited electrolytically from the material of the electrodes, and 50 cc of Prussian blue solution (10% formalin saturated with potassium ferrocyanide) was injected into the heart. The brain was removed and stored in the same solution for 24 hours. The brain was then sectioned with a freezing microtome, and the Prussian blue marked structures identified histologically.

RESULTS

As a result of this investigation, modification of the names of the various components of the posterior accessory optic tract—transpeduncular tract was found to be necessary (fig. 1). The nerve-fiber bundle which runs from the retina to a synapse located just anterior to the superior colliculus will be called the posterior accessory optic tract. Its nucleus of termination is the nucleus of the posterior accessory optic tract. The nerve-fiber bundle which runs from this nucleus transversely over the cerebral peduncle will be called the transpeduncular tract. Its nucleus of termination is found at the base of the midbrain and is the nucleus of the transpeduncular tract.

Photic response from optic nerve and nucleus of transpeduncular tract. The response of the optic nerve to photic stimulation is shown in figure 2*A*. The mean latency of the 'on' response was found to be 17.9 msec., while the mode latency was equal to 15 msec. (N-31).

The responses evoked from the nucleus of the transpeduncular tract by photic stimulation are shown in figure 2*B*. The mean latency of the 'on' response was 27.4 msec. with a range from 20 to 45 msec. The modal latency was 23 msec. and is probably a more meaningful value.

Simultaneous recordings from the optic nerve and the nucleus of the transpeduncular tract during photic stimulation are shown in figure 2*C*. These recordings were obtained from an encéphale isolé preparation. Note the lack of the 'off' response from the nucleus of the transpeduncular tract. In only 3 of the 35 rabbits was an 'off' response, of small amplitude, ever found.

The photic responses from the optic nerve, superior colliculus and the nucleus of the transpeduncular tract exhibited adaptation—a decrease in the amplitude of the response following a prior photic stimulus. It can be demonstrated repeatedly and a very short rest was sufficient to eliminate the adaptation and restore higher amplitude responses.

Response elicited from nucleus of transpeduncular tract by electrical stimulation of optic nerve. Recordings of the responses elicited from the nucleus of the transpeduncular tract by electrical stimulation of the optic nerve are shown in figure 3. The latency of the response was found to range from 1.0 to 3.0 msec. with a mean of 1.7 msec. The form of the response was either monophasic or biphasic.

The recordings shown in *A* and *B* were obtained from urethane preparations, while those in *C* and *D* were from an encéphale isolé preparation. *B* is a photographically averaged record: the shutter of the camera was held open, and the beam of the oscilloscope was allowed to sweep

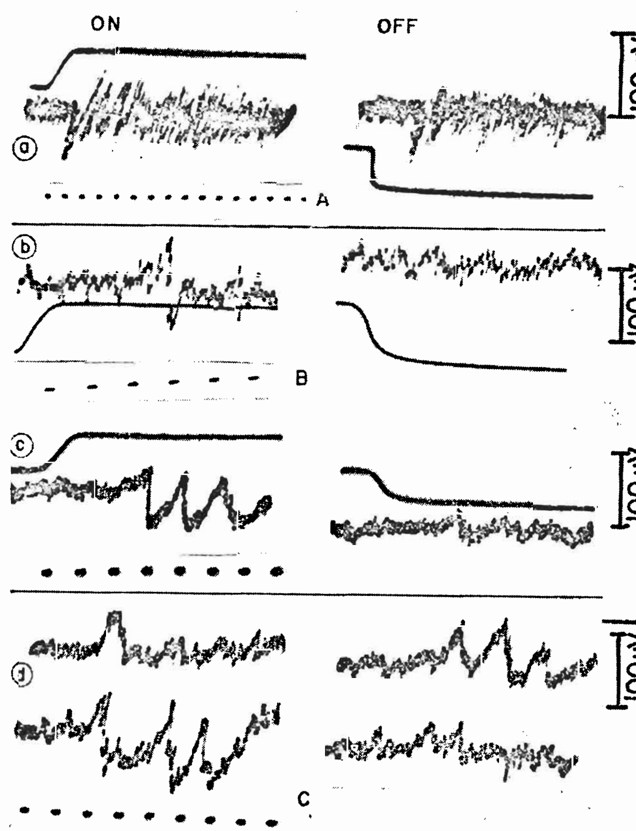

FIG. 2. *A*. On-off light response from the optic nerve. Time = 10 msec., calibration pulses = 100 µv. Amplifier time constant = 0.01 sec., upper frequency limit at half-amplitude response = 4 kc. *B*. On-off light response from the nucleus of the transpeduncular tract. Time units = 10 msec., calibration pulses = 100 µv. Amplifier setting as in *A*. *C*. Simultaneous recording from the optic nerve (*ON*) and the nucleus of the transpeduncular tract (*NTPT*). Recordings from an encéphale isolé preparation. Time units = 10 msec., calibration pulses = 100 µv. Amplifier setting as in *A*.

across the film approximately 40 times. *D* is a d.c. recording at slow sweep speed of the oscilloscope trace. The time units are 10 msec. This d.c. recording shows that there are no slow-rising and/or late-occurring waves.

The refractory period (because of the presence of a synapse in this pathway, this is not a measure of the conventional refractory periods of nerve fibers) of the pathway from the optic nerve to the nucleus of the transpeduncular tract was measured. With short interstimuli intervals only one response was seen. The 'absolute refractory period' of this pathway was found to be 0.8–1.0 msec. while the relative refractory period varied from 2.0 to 2.5 msec.

Encéphale isolé preparations. The encéphale isolé preparations were used to determine whether the urethane anesthesia was affecting any of the responses. Responses to photic and electrical stimulation were compared with similar responses obtained under urethane anesthesia. As a final check, urethane was administered to the encéphale isolé animal and the responses before and after the administration were compared.

Recordings from one of the encéphale isolé preparations have been included in the previous figures (2*C*, 3*C*, 3*D*, 4*A* and 4*B*). No differences could be observed. Also, no apparent changes in the responses were noted with the administration of urethane to the encéphale isolé animal.

Ipsilateral stimulation. All of the responses reported to this point were obtained from contralateral stimulation. Ipsilateral fibers have been reported to be present in the rabbit (5, 6). Such fibers should be capable of being detected by physiological techniques.

To test for ipsilateral fibers, the electrode was placed in the nucleus of the transpeduncular tract using contralateral stimulation. The beam of light was then reflected into the ipsilateral eye. With electrical stimulation, the optic fibers were stimulated intraorbitally to insure the stimulation of only ipsilateral fibers.

Comparable contralateral and ipsilateral stimulation records are shown in figure 4*A*. The response from the

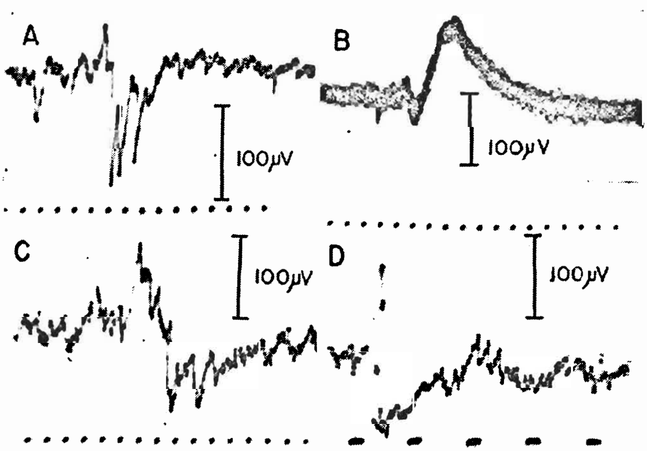

FIG. 3. Responses evoked from the nucleus of the transpeduncular tract by electrical stimulation of the optic nerve. Time units = 1 msec., calibration pulses = 100 μv.

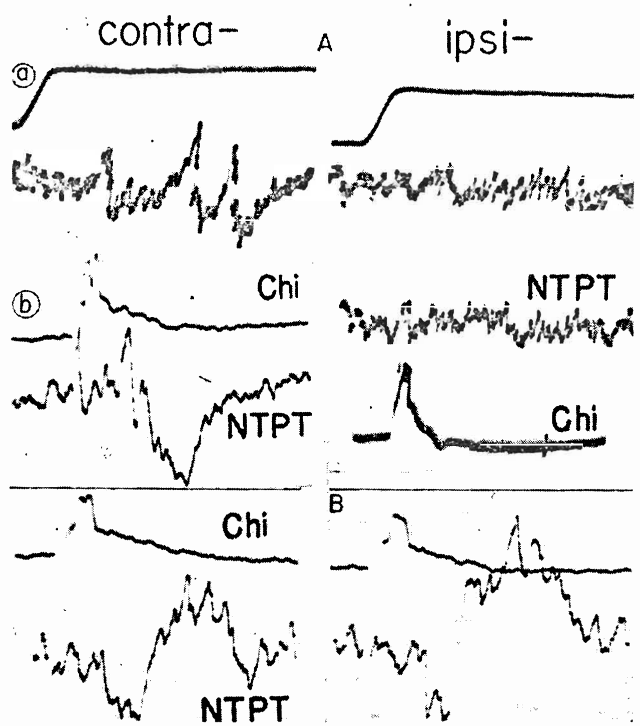

FIG. 4. *A*. Comparison of contralateral and ipsilateral stimulation. *a*, response evoked from the nucleus of the transpeduncular tract by photic stimulation. *b*, stimulation of the optic fibers intraorbitally and responses from the chiasma (*Chi*) and the nucleus of the transpeduncular tract (*NTPT*). *B*. Response from the chiasma and the nucleus of the transpeduncular tract before (*I*) and after (*II*) tetanic stimulation of the optic fibers intraorbitally.

nucleus of the transpeduncular tract to photic stimulation is shown in *row a* while the response to electrical stimulation is shown in *row b*. The response from the electrode in the chiasma (Chi) is also shown.

As expected, large amplitude responses were evoked by contralateral stimulation. Ipsilateral stimulation, on the other hand, failed to elicit a response from the nucleus of the transpeduncular tract. The response from the chiasma indicated that the electrode in the eye was stimulating optic fibers.

Photic and electrical stimulation also failed to elicit a response from either the ipsilateral lateral geniculate nucleus or the superior colliculus.

Nucleus of posterior accessory optic tract. Electrical stimulation of the nucleus of the transpeduncular tract failed to elicit a response from the optic nerve. A response often seen was found to disappear with a curarizing agent (Flaxedil), and has been found to be an artifact arising from the extraocular muscles (7).

The lack of a response from the optic nerve indicated that a synapse must be interposed between the optic nerve and the nucleus of the transpeduncular tract. The presence of the synapse was confirmed by posttetanic potentiation and also by the effects of asphyxia.

The effect of tetanic stimulation of the optic fibers intraorbitally on the response from the chiasma and the nucleus of the transpeduncular tract is shown in figure

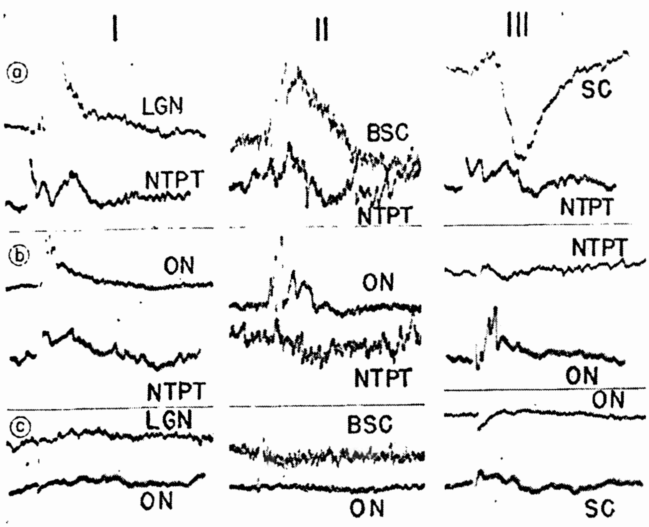

FIG. 5. Relationship of the nucleus of the transpeduncular tract to the lateral geniculate nucleus (*column I*), to the optic fibers of the brachium of the superior colliculus (*column II*) and to the superior colliculus (*column III*). See text for explanation.

4*B*. Potentiation is noted in the response from the nucleus of the transpeduncular tract but is absent in the response from the chiasma.

Under the same recording conditions, asphyxia was found to depress the response from the nucleus of the transpeduncular tract after 2.5 minutes. The response from the chiasma after this period was not affected. Three minutes after the resumption of artificial respiration, the response from the nucleus of the transpeduncular tract had returned to its former level.

The indicated synapse has been named the nucleus of the posterior accessory optic tract. A series of experiments was designed to locate this nucleus.

As usual, electrodes were placed in the optic nerve and in the nucleus of the transpeduncular tract. A third electrode was then introduced into various parts of the visual system. By stimulating each in turn and recording from the other two electrodes, it was possible to determine the relationship of these structures to the nucleus of the transpeduncular tract.

1. Lateral geniculate nucleus. The third electrode was placed in the lateral geniculate nucleus. The recordings from one experiment are shown in figure 5, *column 1*.

In *a*, the optic nerve was stimulated. A response was evoked from the lateral geniculate nucleus (LGN) and the nucleus of the transpeduncular tract (NTPT). In *b*, the lateral geniculate nucleus was stimulated. A response was elicited from the optic nerve (ON) but none from the nucleus of the transpeduncular tract. In *c*, the transpeduncular tract nucleus was stimulated. A response was not elicited from either the optic nerve or the lateral geniculate nucleus.

These observations indicate that the lateral geniculate nucleus is not a part of the posterior accessory optic tract—transpeduncular tract pathway.

2. Brachium of superior colliculus. The third electrode was placed in the optic fibers which make up the brachium of the superior colliculus. The recordings from one experiment are shown in *column II* of figure 5.

In *a*, the responses evoked from the brachium of the superior colliculus (BSC) and nucleus of the transpeduncular tract by stimulating the optic nerve are shown. In *b*, the brachium of the superior colliculus was stimulated. A response was evoked from the optic nerve but none was obtained from the nucleus of the transpeduncular tract. In *c*, the transpeduncular tract was stimulated. A response could not be elicited from either the optic nerve or the brachium of the superior colliculus.

From these findings it can be concluded that the fibers of the posterior accessory optic tract—transpeduncular tract are not among the optic fibers which make up the brachium of the superior colliculus.

3. Superior colliculus. The third electrode was placed in the superior colliculus. The recordings from one experiment are shown in *column III* of figure 5.

In *a*, the optic nerve was stimulated. A response was evoked from both the superior colliculus (SC) and the nucleus of the transpeduncular tract. In *b*, the recordings obtained during the stimulation of the superior colliculus are presented. A response was evoked from the optic nerve but none from the nucleus of the transpeduncular tract. In *c*, the nucleus of the transpeduncular tract was stimulated. A response was not elicited from either the optic nerve or the superior colliculus.

It therefore appears that the superior colliculus is not part of the posterior accessory optic tract—transpeduncular tract. Also, there is no evidence for a direct nerve-

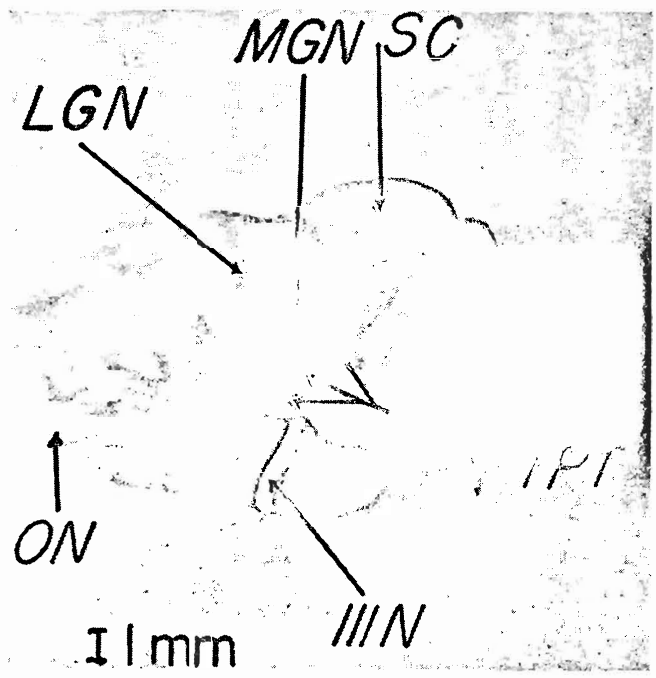

FIG. 6. Photograph of the lateral aspect of the brain stem of a rabbit. *ON*—optic nerve; *LGN*—lateral geniculate nucleus; *SC*—superior colliculus; *MGN*—medial geniculate nucleus; *III N*—oculomotor nerve; *TPT*—transpeduncular tract.

fiber connection between the superior colliculus and the nucleus of the transpeduncular tract.

4. Nucleus of posterior accessory optic tract. A photograph of the lateral aspect of the brain stem of a rabbit is shown in figure 6. The transpeduncular tract (TPT) can be best seen as it runs transversely over the cerebral peduncle. If it is followed dorsally it can be seen to course posterior to the medial geniculate nucleus (MGN) and disappear just anterior to the superior colliculus. Ventrally it can be seen to disappear under the cerebral peduncle between the mammillary body and the oculomotor nerve (III N).

The cerebral cortex over the superior colliculus was scooped out and the third electrode was placed just anterior to the superior colliculus. Recordings from two experiments are shown in figure 7, *columns I* and *II*.

In *a*, the recordings obtained during the stimulation of the optic nerve are shown. A response was elicited from the nucleus of the posterior accessory optic tract (NPAOT) and the nucleus of the transpeduncular tract. In *b*, the nucleus of the posterior accessory optic tract was stimulated. A response was elicited from the optic nerve and the transpeduncular tract nucleus. In *c*, the nucleus of the transpeduncular tract was stimulated. As expected, a response could not be elicited from the optic nerve but a small and definite response was recorded from the nucleus of the posterior accessory optic tract. A photographically averaged record of the response from the nucleus of the posterior accessory optic tract is shown in *Id*. In *IId*, the lower trace of *IIc* is shown at a higher gain.

The responses evoked from the nucleus of the posterior accessory optic tract by photic stimulation are shown in

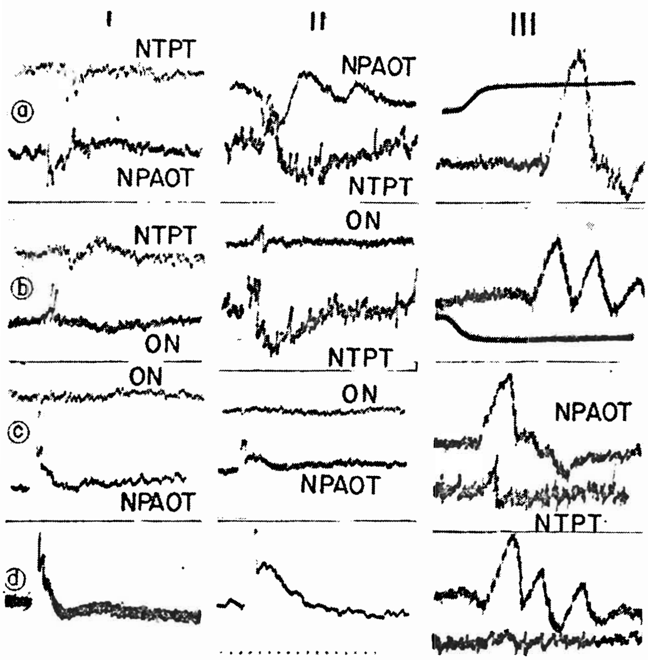

FIG. 7. Functional relationship of the nucleus of the posterior accessory optic tract to the nucleus of the transpeduncular tract. Electrical stimulation records in *columns I* and *II*. Photic stimulation records in *column III*. Records in *columns II* and *III* were obtained from the same rabbit. See text for explanation.

column III. The records shown in *II* and *III* were obtained from the same rabbit. The 'on' response is shown in *a* and the 'off' response is shown in *b*. Simultaneous recordings of the 'on' and 'off' responses from the nucleus of the transpeduncular tract and the nucleus of the posterior accessory optic tract are shown in *c* and *d*, respectively.

Histological studies. Each brain was sectioned with the freezing microtome. The sections containing the Prussian blue mark were examined to determine the exact anatomical site of the recordings.

Figure 8*A* is a photograph of a normal brain section prepared by the Nissl method. The nucleus of the transpeduncular tract is located ventrolateral to the red nucleus (RN) and dorsal to the cerebral peduncle (CP). The anterior portion of the oculomotor nucleus (III Nn) can also be seen.

Figure 8*B* is a photograph of a rabbit brain section prepared by the Marchi technique (slide prepared by R. Giolli, Dept. of Anatomy, Univ. of Calif. Berkeley, 1959). The rabbit had had both eyes enucleated and was sacrificed 2 weeks after the operation. The degeneration granules can be seen in the optic tracts as well as in the transpeduncular tract.

Figure 8*C* shows a brain section from which electrical recordings were obtained. It was prepared by the Nissl method. The dark spot in the nucleus of the transpeduncular tract is the Prussian blue mark. All of the encéphale isolé recordings which have been presented were obtained from this rabbit.

Figure 8*D* is a photograph of a brain section from another rabbit from which electrical recordings were obtained. Two Prussian blue marks can be seen. The more ventral one is located in the nucleus of the transpeduncular tract. The more dorsal mark is the site of the nucleus of the posterior accessory optic tract. Recordings from this animal are shown in *columns II* and *III* of figure 7.

DISCUSSION

There is no doubt that the response recorded from the midbrain originated from the nucleus of the transpeduncular tract. The histological examination of the brain sections showed that the recordings were made from the region described by the anatomical investigators as the site of the nucleus of the transpeduncular tract.

The photic response from the nucleus of the transpeduncular tract is unique. It is mainly an 'on' response. The 'off' response is relatively weak when it is present at all. The significance of this is yet to be determined.

The phenomenon of adaptation has been shown to occur in the 'on' responses from the optic nerve, the superior colliculus, and the nucleus of the transpeduncular tract. It was not necessary to dark-adapt the eye to demonstrate this adaptation. It can be demonstrated repeatedly and a very short rest (1.5 sec.) was sufficient to eliminate the adaptation and restore higher amplitude responses.

Two observations indicate that this adaptation is a retinal phenomenon. First, it is observed in the 'on' re-

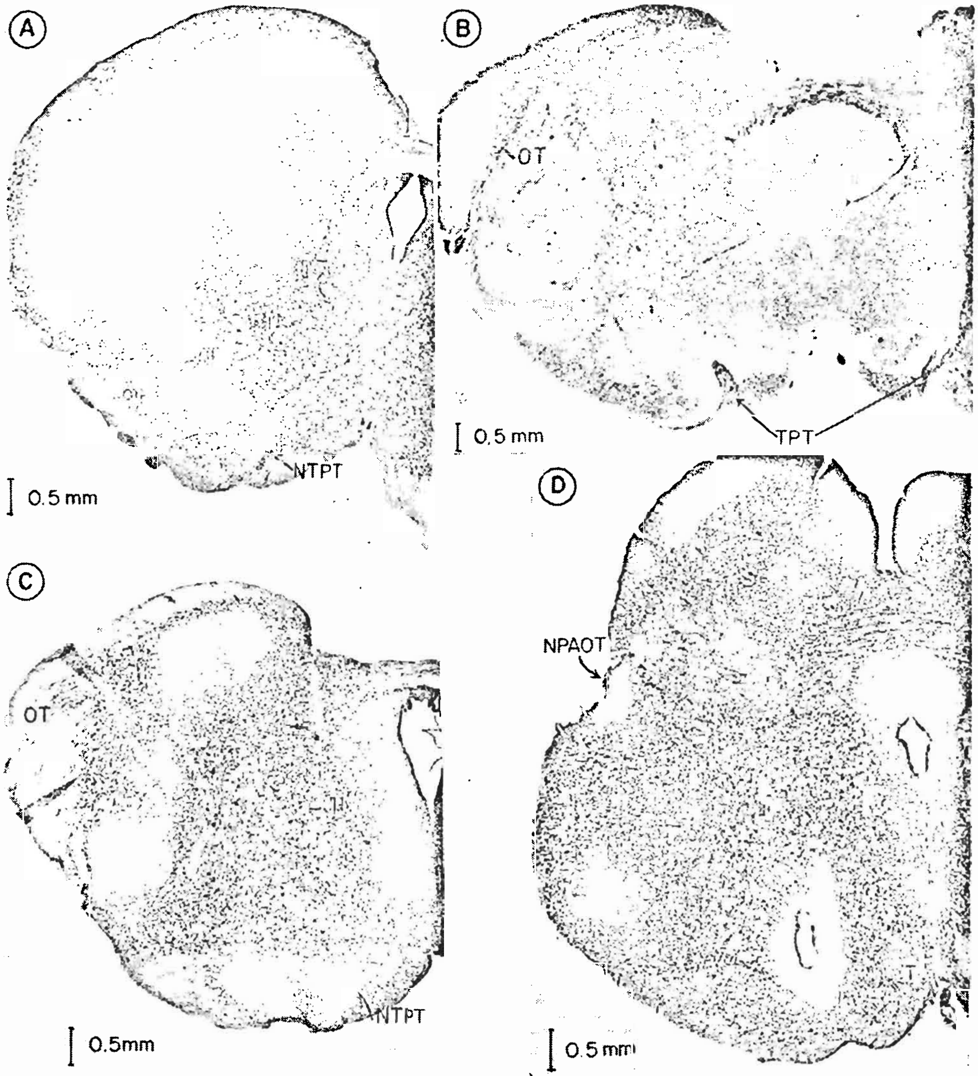

FIG. 8. *A:* photograph of a normal brain section of a rabbit prepared by the Nissl method. *B:* photograph of a rabbit's brain section prepared by the Marchi method. Note the degeneration granules in the optic tract and and the transpeduncular tract. *C:* photograph of a rabbit's brain section prepared by the Nissl method. Note the Prussian blue mark in the transpeduncular tract nucleus. *D:* photograph of a rabbit's brain section prepared by the Nissl method. Note the two Prussian blue marks. Ventral one is located in the nucleus of the transpeduncular tract. Dorsal mark is located in the nucleus of the posterior accessory optic tract. *OT*—optic tract; *MGN*—medial geniculate nucleus; *CP*—cerebral peduncle; *III Nn*—oculomotor nucleus; *RN*—red nucleus; *SN*—substantia nigra; *TPT*—transpeduncular tract; *NPAOT*—nucleus of the posterior accessory optic tract.

sponse from the optic nerve. Second, adaptation cannot be shown in responses of the nucleus of the transpeduncular tract elicited by electrical stimulation of the optic nerve. The rapidity with which the adaptation can be eliminated indicates that it has a neural rather than a photochemical basis.

The response evoked from the nucleus of the transpeduncular tract by electrical stimulation of the optic nerve behaved as a typical nerve-fiber bundle response. The fact that the response was not affected by Flaxedil indicated that it was not related to any neuromuscular event. The presence of the 'on' response showed that the fibers of the posterior accessory optic tract—transpeduncular tract are retinal in origin. This eliminates the possibility that the response from the midbrain originated from nonoptic fibers, e.g. fibers of the supraoptic commissures, which pass near the chiasma and end in the midbrain (8–10).

The absolute refractory period of the pathway from the optic nerve to the transpeduncular tract nucleus was found to be 0.8–1.0 msec. Although there is a synapse in this pathway, the refractory period still falls within the range given for myelinated *A* fibers (11). This, then, agrees with the anatomical investigators who reported that all of the fibers of this pathway were myelinated.

The experiments conducted to detect the presence of ipsilateral fibers were all negative. The contralateral stimulation records demonstrated that the electrode was favorably situated in the structures investigated, i.e. the lateral geniculate nucleus, the superior colliculus, and the transpeduncular tract. One possible criticism of these experiments is that the electrode may not have been situated in the exact area where ipsilateral fibers terminated. However, ipsilateral stimulation was performed in many rabbits and a good sampling of the structures was obtained. In no case was an ipsilateral response evoked. Therefore, if ipsilateral fibers are present in the rabbit, the number appears to be so small that a recordable response cannot be elicited.

The fact that a response could not be evoked from the optic nerve by the electrical stimulation of the nucleus of the transpeduncular tract disclosed that a synapse must be situated between these two points. The potentiation of the response evoked from the nucleus of the transpeduncular tract when the optic nerve is stimulated tetanically indicated that this response is a postsynaptic response (12). The greater susceptibility of the synapse, than the nerve fibers, to asphyxia also verified the presence of the synapse (13). This synapse is the nucleus of the posterior accessory optic tract.

The fibers of the posterior accessory optic tract—transpeduncular tract appear not to pass through the lateral geniculate nucleus. This supports the anatomical investigators who have reported that this pathway separates from the main optic tract anterior to the lateral geniculate nucleus.

The observation made on the superior colliculus supported prior anatomical investigators. von Gudden (14) showed that destroying the superior colliculus did not affect the transpeduncular tract. Marburg (15) and Wallenberg (16), independently, were not able to find any nerve fiber connection between the superior colliculus and the nucleus of the transpeduncular tract.

The nucleus of the posterior accessory optic tract was found to be located on the lateral aspect of the midbrain. It is located just dorsal to the medial geniculate nucleus and ventral to the superior colliculus. In the anterior-posterior direction, it is located at the posterior border of the medial geniculate nucleus.

This places the nucleus of the posterior accessory optic tract in the region of the suprageniculate nucleus. The parageniculate nucleus is also situated in this region. Whether the nucleus of the posterior accessory optic tract is part of the suprageniculate nucleus or of the parageniculate nucleus, or a separate nucleus will have to be determined by histological studies.

Transynaptic degeneration of the neurons in the lateral geniculate nucleus has been reported to be a very slow process in the rabbit (17). Yet the transpeduncular tract, a transynaptic pathway, shows degenerative changes in seven days. This interesting and unexpected finding gives rise to several questions about the histology and physiology of the nucleus of the posterior accessory optic tract. Investigation is being conducted to answer these questions.

Very little can be said at this time about the function of the posterior accessory optic tract—transpeduncular tract. It is possible, however, to reject several proposals by others.

Stimulation of the nucleus of the transpeduncular tract did not appear to change the pupil size or the curvature of the crystalline lens (as measured with a skiascope). Edinger (18) had reported that the nucleus of the transpeduncular tract was part of the ciliary ganglion that had failed to migrate orbitally. Massaut (19) stated that the transpeduncular tract probably contained pupillary fibers. Our findings do not support either of these two ideas.

Pressing on the eye or pulling on the extraocular muscles did not elicit any recordable potentials from the nucleus of the transpeduncular tract. Thus, the nucleus does not appear to be a proprioceptive station.

No centrifugal fibers appear to run from the nucleus of the transpeduncular tract to the retina via the optic nerve, although Münzer and Wiener (20) and also Tsang (21) thought that this pathway contained both centrifugal and centripetal fibers. Whether centrifugal fibers exist, which originate or pass through the nucleus of the posterior accessory optic tract, is still to be determined.

The posterior accessory optic tract—transpeduncular tract appears from a morphological viewpoint to be a part of a photic pathway to the reticular formation. The search for evidence which will clarify the function of this pathway will be continued.

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