THE ACCESSORY OPTIC SYSTEM*

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Classically, three pairs of retinal projections to the brain are described: to the lateral geniculate body, to the superior colliculus, and to the pretectal nucleus. In our laboratory we have been studying the less-known accessory optic system which projects from the retina to the midbrain. Three pairs of such tracts have been described: the anterior accessory optic tracts (Bochenek), the posterior accessory optic tracts (*tractus peduncularis transversus* of Marburg), and the transpeduncular tracts (*tractus peduncularis* of Gudden). In present day nonmammalian vertebrates these paths are represented by only one discreet pair of tracts, the basal optic roots. Thus the accessory optic system is known in all classes of vertebrates.[1]

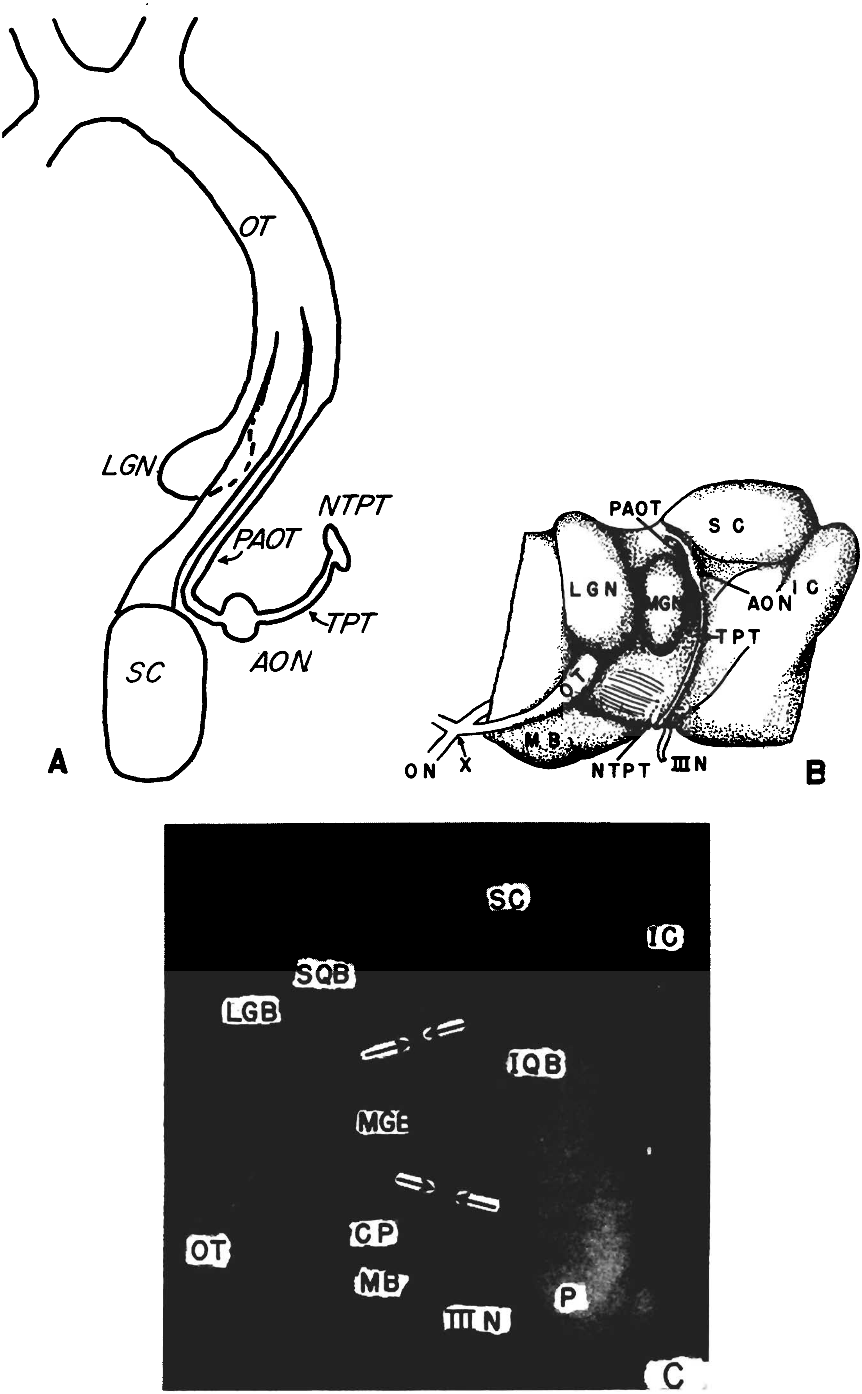
It might be asked, is the accessory optic system a possible (or probable) photo-neural input for the triggering of circadian or other rhythms? In attempting to answer this question we shall draw largely on research done in our laboratory by Roland A. Giolli, Duco I. Hamasaki, Richard M. Hill, Roc E. Walley, and myself.

History

The transpeduncular tract was first described in 1870 by Gudden[2] who later showed that it contained fibers projected from the retina.[3] This tract emerges from the superior quadrigeminal brachium, courses ventrally over the surface of the cerebral peduncle traversing it to its ventromedial aspect where it "horseshoes" to a nucleus in the tegmentum as first described by Bechterew.[4] The nucleus is lateral to the mammillary peduncle and the lateral mammillary nucleus as well as the exit of the third cranial nerve. It is ventral to the red nucleus and medial to the substantia nigra and cerebral peduncle. A number of investigators have studied the transpeduncular tracts in the intervening century and are broadly in accord with the original description despite many transformations of nomenclature.

The fibers of the posterior accessory optic tracts originate in the retina and were first described at the turn of the century by Marburg[5] (who called them the *tractus peduncularis transversus*) as leaving the optic tract just before it reaches the lateral geniculate body. The tracts pass over the cerebral peduncles, and continue as Gudden described the pathway.

*Supported by grants from the National Science Foundation.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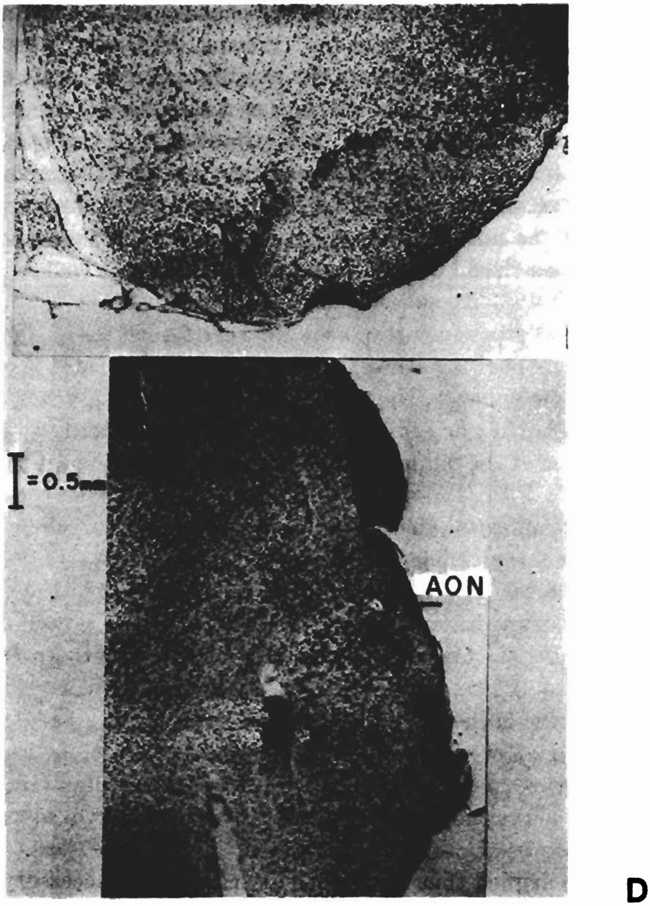

FIGURE 1. The functional accessory optic system of the rabbit. (*a*) Schematic diagram consisting of the posterior accessory optic tract (PAOT), the accessory optic nucleus (AON, also called the nucleus of the posterior accessory optic tract, PAOT), the transpeduncular tract (TPT) and the nucleus of the transpeduncular tract. (NTPT). Also shown are the optic tract (OT), the lateral geniculate nucleus (LGN) and the superior colliculus (SC). (*b*) The superficial parts of the accessory optic system. Designations as in *a*. (*c*) Photograph of the lateral aspect of the rabbit brain showing the transpeduncular tract between arrows. (*d*) The functional accessory optic system of the rabbit. Transverse sections of the rabbit brain showing marks made at the site of recording. In the upper photograph the mark at the *arrow* is in the nucleus of the transpeduncular tract. Note its position in relation to the substantia nigra (SN) and the cerebral peduncle (CP). In the lower photograph the accessory optic nucleus (AON) is similarly shown in relation to the medial geniculate nucleus (MGN).

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Discussion of the Paper

SHAUL FELDMAN: Have you seen in your section any projections to the anterior regions like the hypothalamus; have you anything to confirm Knocke, and further have you recorded any latencies on this anterior region? I can confirm your latencies in the midbrain because in the cat one can record latencies of 40 or 50 milliseconds. I think Harmon and Berry have reported the same latencies in the cat midbrain. I wonder if you had anything more?

ELWIN MARG (*University of California, Berkeley, Calif.*): Our histological investigations in the rabbit show we have not been able to find any direct connections with the hypothalamus or with structures leading to the cular tract to stimulation of the chiasma demonstrate the synapse by frequency response, post–tetanic–potentiation, and response to asphyxia.

Current study of the accessory optic system in an Old World monkey (the Cynomolgus)[11] points to a release from our anatomic–physiological dilemma. This higher primate does not have an anterior accessory optic tract. Ocular enucleation leads to crossed Wallerian degeneration only as far as the nucleus of the posterior accessory optic tract, which now may be

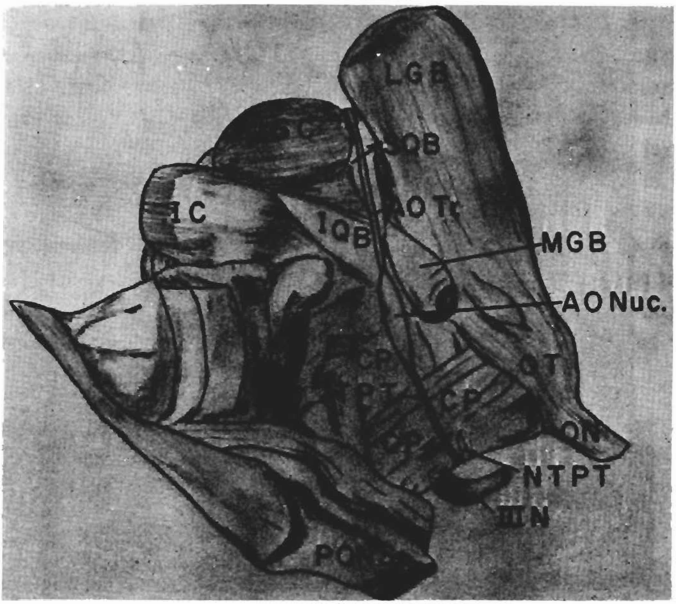

FIGURE 2*a*. The accessory optic system in the monkey. Diagram with the same designations as in FIGURE 1 except that the accessory optic nucleus is AONuc and the posterior has been dropped from the accessory optic tract (AOTr).

termed simply the accessory optic nucleus of the accessory optic tract (FIGURE 2).

Our anatomic-physiological dilemma may be resolved by postulating that both the anterior accessory optic tract and the direct fibers of the posterior accessory optic tract to the nucleus of the transpeduncular tract are largely, if not entirely, nonfunctional in the rabbit, and altogether absent in the primate (as indeed they are in lower vertebrates). On this basis, the accessory optic-transpeduncular tracts which comprise the known accessory optic system are functionally similar in rabbits and monkeys.

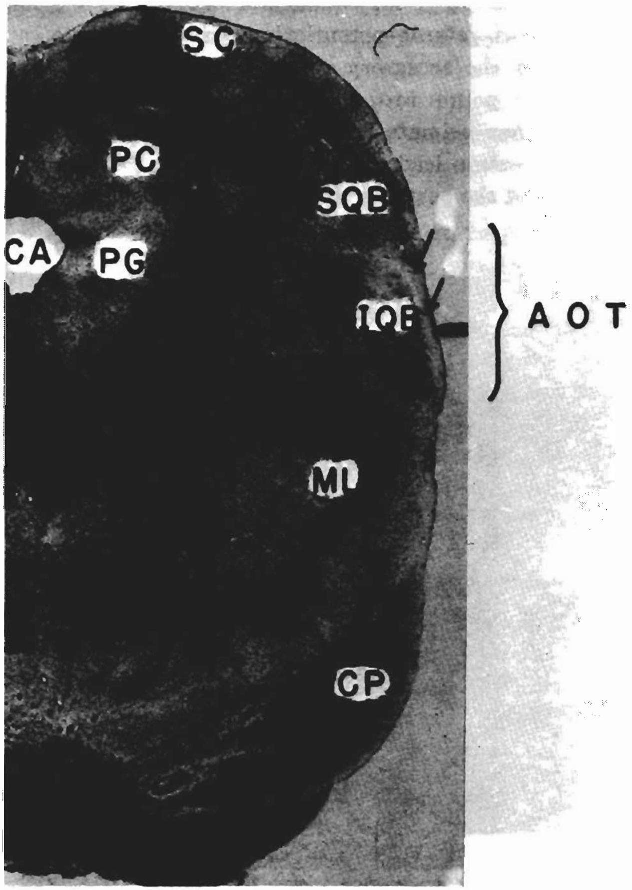

FIGURE 2*b*. The accessory optic system in the monkey. The accessory optic tract (AOT) is shown by the four *arrows*.

It should be noted that the transpeduncular tract has been clearly demonstrated in the human brain by Marburg[5c] (FIGURE 3).

Our Investigations of the Neurophysiological Characteristics of the Accessory Optic System

Macro- and micro-electrode recordings from the nucleus of the transpeduncular tract have demonstrated a number of characteristics unique in the visual system in the coding of information from the retinal photoreceptors.[7,8,9]

Macroelectrode recordings from the system yield primarily an *on* response when the light stimulus is applied to the eye, with little or no *off* when the stimulus ceases, unlike the apparently equal *on-off* found in the other visual pathways. Subsequent microelectrode recordings showed two kinds of unit responses: *on* and *on-off*, in which the *off* moiety was much the smaller (FIGURE 4). Rarely was a pure *off* unit response observed.

The frequency response to reiterative light stimuli, with a 50 per cent duty cycle, was notable because of a band-stop-filter effect ranging from about 2 to 10 cps (FIGURE 5).

Although the receptive field of the accessory optic system in the rabbit can be found over the whole retina, the field is more densely represented in the area centralis.

If the recording electrode is shifted from the nucleus of the transpeduncular tract to the accessory optic nucleus (or nucleus of the posterior accessory optic tract), the same unique characteristics are observed. Thus the unique responses summarized above are not a result of activity in the accessory optic nucleus but in a more distal cell station, that is, in the retina.

The receptive fields of single units of the nucleus of the transpeduncular tract are approximately five to ten times larger in diameter than those of the lateral geniculate body (FIGURE 6).[12] The majority of these units also show directional selectivity to moving stimuli similar to that of the re-

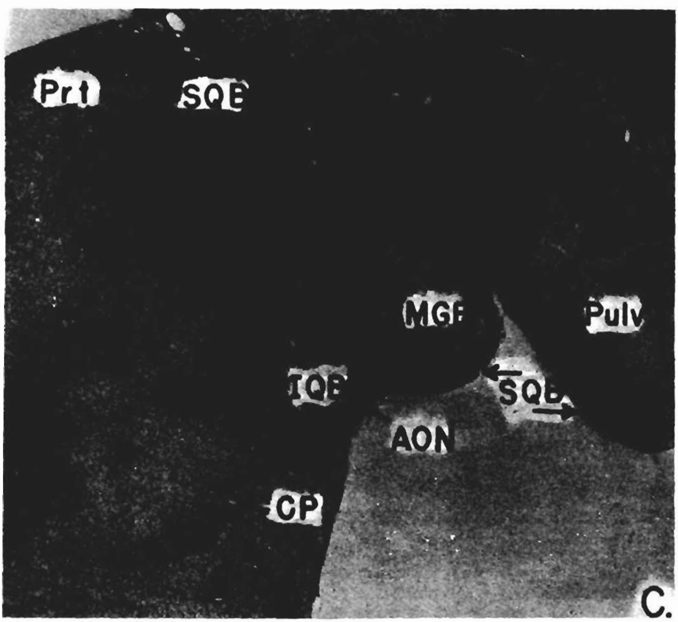

FIGURE 2*c*. The accessory optic system in the monkey. The accessory optic nucleus (AON) is shown adjacent to the inferior quadrigeminal brachium (IQB).

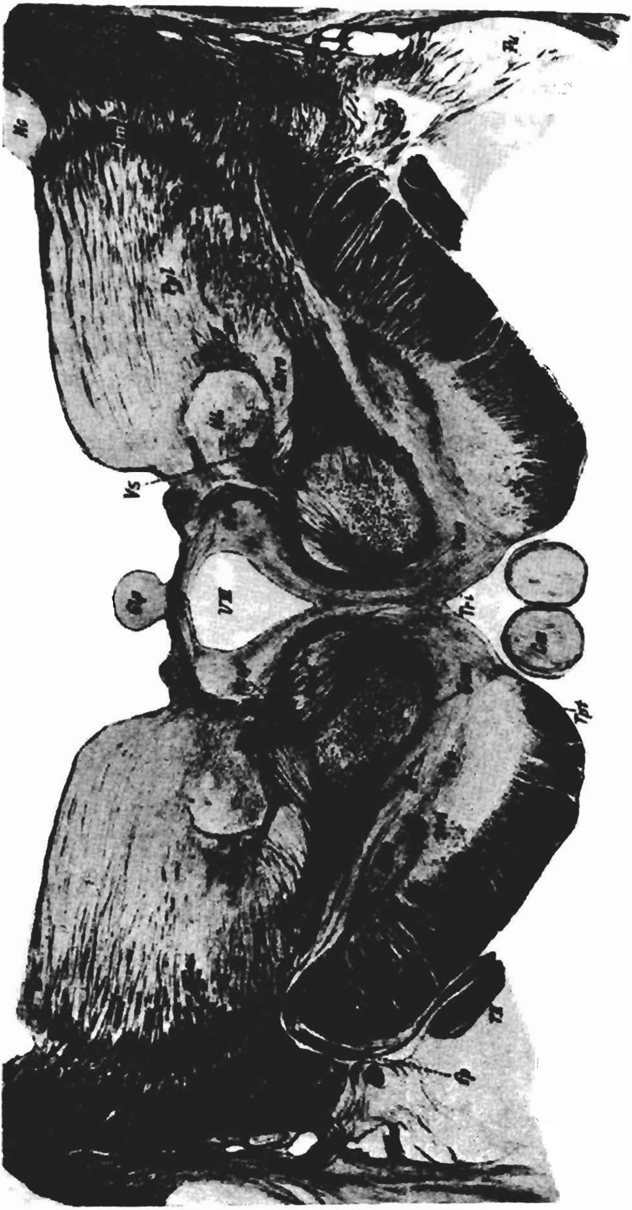

FIGURE 3. Transverse section of the human brain showing the transpeduncular tract (*Tpt*), Marburg.[5c]

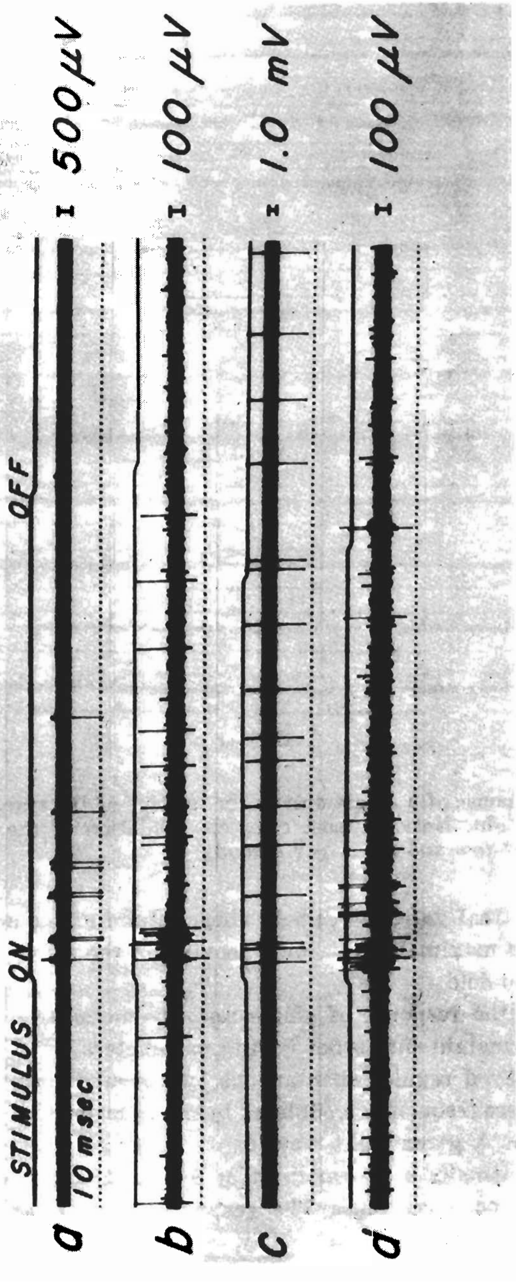

FIGURE 4. Single units recorded from the nucleus of the transpeduncular tract to photic stimulation of the eye. (*a*) and (*b*) *On* response of single units. (*c*) and (*d*) *On-Off* response of single units. Note that the *on* response is greater than the *off*.

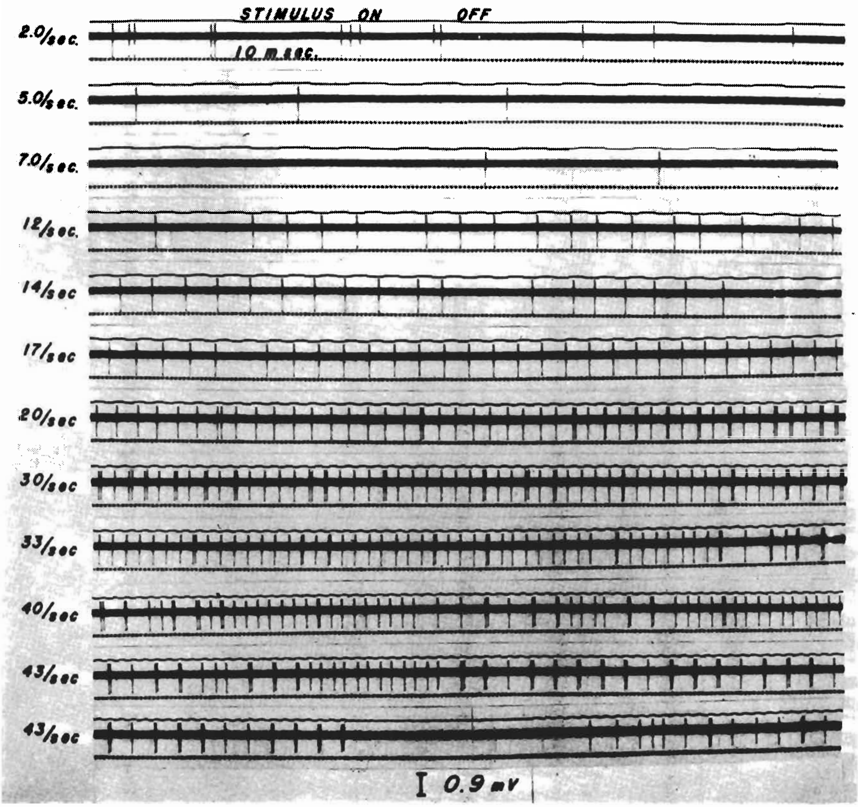

FIGURE 5. The response of a single unit in the nucleus of the transpeduncular tract to flickering light. Notice almost complete inhibition of the response at photic frequencies of five and seven per second.

ceptive fields of retinal ganglion cells.[13] They differ in that nearly all of these units respond maximally to stimuli moving in the same direction — upward in the visual field.

Investigation of the response of single units to monochromatic stimulation provided an insight into other coding parameters.[13, 14] Slightly over half the cells displayed regular spontaneous background activity of 14 to 55 per second and were frequently modulated by monochromatic retinal stimulation (FIGURE 7). A given light wavelength could be represented by a response from a normally quiescent unit at which stimulus it exhibited its maximum frequency response. The responses were clearly different from those of the lateral geniculate body in two ways: first, frequency modulation hue coding is rarely seen in the lateral geniculate body of the rabbit; secondly, only two wavelengths of maximum sensitivity predominate in the nucleus (461 and 501 mμ as seen in FIGURE 8) compared to as many as seven in the lateral geniculate body.

Latencies from photic stimulation ranged from 20 to 160 msec.

Hypotheses of the Function of the Accessory Optic System

First hypothesis: The accessory optic system transmits a spatial image to the midbrain tegmentum, as the primary visual pathway does to the lateral geniculate body and occipital cortex in higher vertebrates, and to the tectum in lower vertebrates. The rabbit's transpeduncular tract has 1400 to 2500 fibers from each retina. Compared with the 265,000 fibers found in the optic nerve, it would seem unlikely that the spatial information contained in so relatively few fibers would be of value. The image resolution would be poor indeed, even if the projection were largely from the area centralis. Furthermore, the five to ten fold size of the receptive

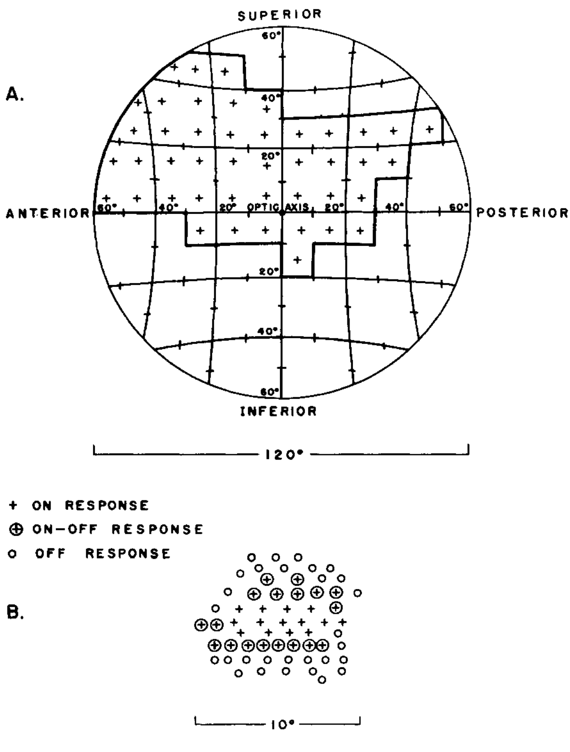

FIGURE 6. + = *on* response; ⊕ = *on-off* response; *O* = *off* response. Comparison of a receptive field of a single unit in the nucleus of the transpeduncular tract (*a*) and in the lateral geniculate nucleus (*b*). Note that the scales are different so that the receptive field in *a* is about 10 times the diameter of that in (*b*).[12]

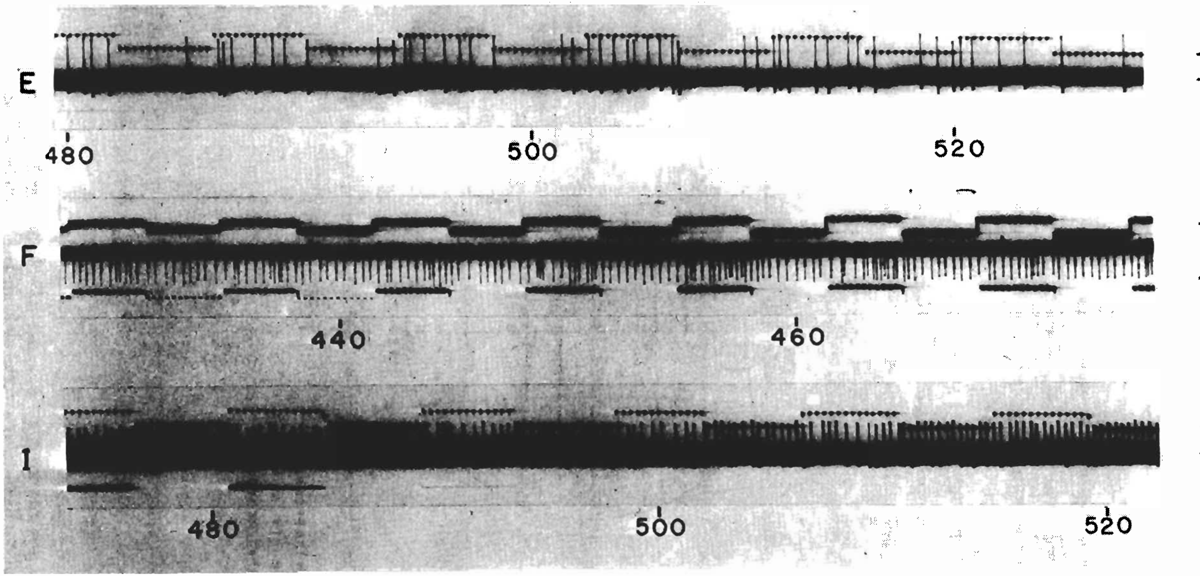

FIGURE 7. The effect of the wavelength of the stimulus on the three kinds of units found in the nucleus of the transpeduncular tract in the rabbit. The excitatory unit (E) behaves as similar units in the lateral geniculate nucleus and elsewhere. The *on* response in this instance is maximum at 501 mμ. The other two units are firing spontaneously, the facilitatory (F) increasing its frequency to a maximum, in this instance, at 461 mμ. The inhibitory (I) unit decreases its spontaneous frequency to a minimum, in this instance, at 501 mμ.

fields of cells in the nucleus compared to those of the lateral geniculate body also reduce the likelihood of a spatial resolution function.

Second hypothesis: The accessory optic system is a hue discrimination center. This has been essentially rejected by finding only two out of seven wavelengths of maximum sensitivity represented in the nucleus.[13, 14]

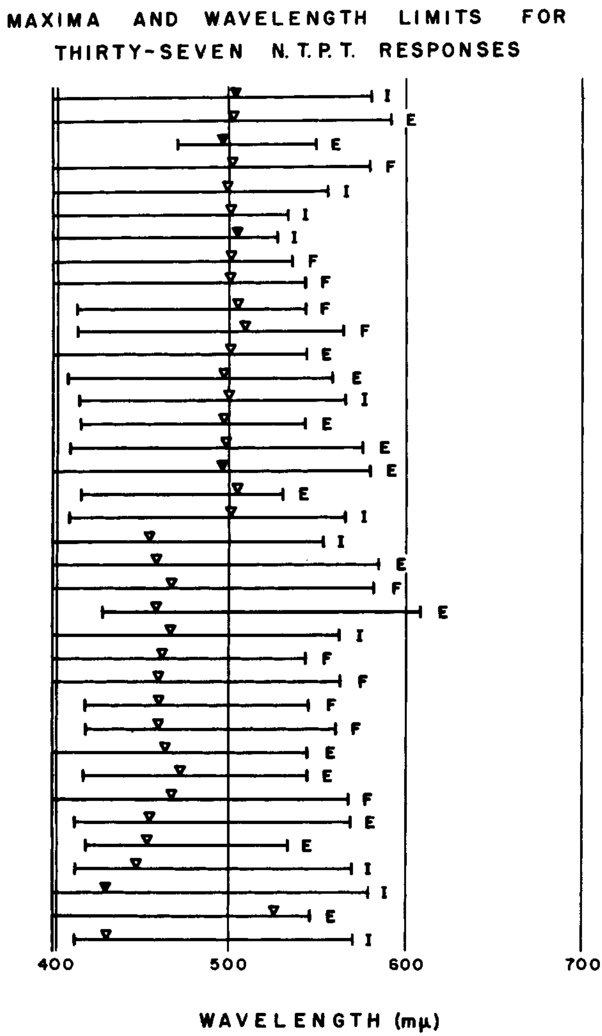

FIGURE 8. Maxima and wavelength limits for thirty-seven N.T.P.T. responses. Regardless of the type of response, maximal wavelength effects were found in the nucleus of the transpeduncular tract grouped at two wavelengths 461 and 501 mμ.

Third hypothesis: The accessory optic system is a relatively direct photic path from the retina to the midbrain reticular formation and tegmentum for possible alerting-arousal phenomena. Supporting this hypothesis is the histology of the nucleus of the transpeduncular tract in the rabbit. Most

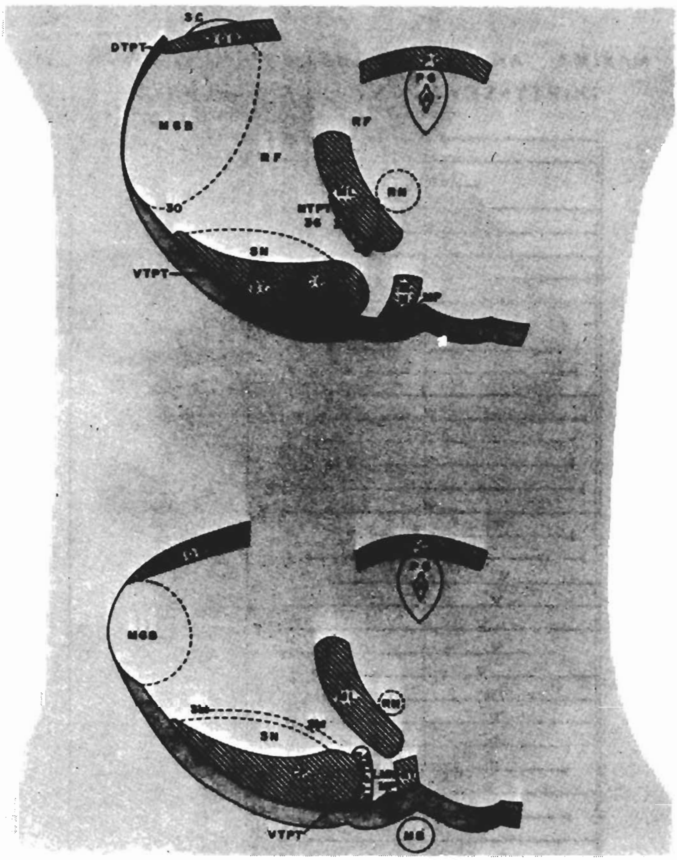

FIGURE 9. Sites of the electrode tips in implanted rabbits. Even with a restricted field of stimulation (adjacent bipolar electrodes and low threshold voltage) no distinction could be made in responses between stimulation in the nucleus of the transpeduncular tract and elsewhere. DTPT and VTPT are dorsal and ventral transpeduncular tracts.

of the efferent fibers from the nucleus fan out dorsally and lose themselves in the tegmentum and reticular formation.

Because of this anatomical evidence, attempts were made to interfere with the function of the nucleus and observe behavioral effects. Prelimi-

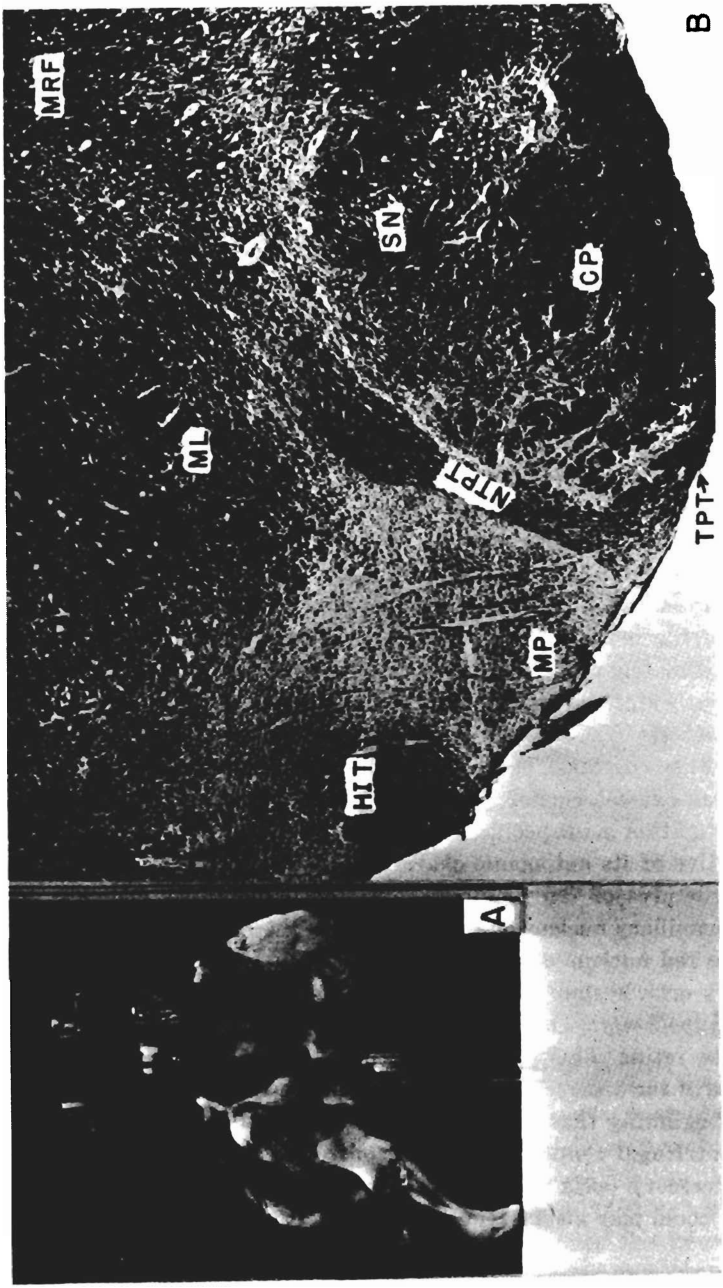

FIGURE 10*a*. Skull, electrodes, and receptacle of an implanted rabbit. Rostral pair of electrodes were in the chiasma. Caudal electrode is a hollow stainless steel needle containing a twisted pair of insulated stainless steel wires. It was in the midbrain. (*b*) The transpeduncular tract (TPT) and its nucleus (NTPT).

nary experiments in observing rabbits with bilateral electrolytic lesions in the nucleus showed no apparent difference from their sham-operated controls. A series of animals were prepared with a pair of stimulating electrodes in a stainless steel shank (FIGURE 9).[15] The rabbits were deprived of sleep the previous night and then stimulated and watched in an isolation observation box. Shocking the nucleus or other points in the midbrain gave typical alerting-arousal responses, both behavioral and electroencephalographic (FIGURE 10). The accessory optic system responds to stimulation as does the brain stem reticular formation and other tegmental structures. If these structures form an activating system, then it appears that the accessory optic system provides a photo-activation pathway. The essentially *on* or excitatory nature of the photic response would tend to support this concept. Activation, however, need not be the exclusive function.

Fourth hypothesis: The accessory optic system is an afferent link of the intrinsic or extrinsic oculomotor system. Stimulation of the nucleus of the transpeduncular tract in undrugged animals, restrained only by the confines of the observation box, produced no specific pupillary or eye movements.[15] Therefore this hypothesis is not tenable.

Fifth hypothesis: Because of the upward vertical motion sensitivity of the receptive fields, it has been proposed that the system might provide postural information on changes in the position of the eyes relative to the horizon.[12] Furthermore, the region of the brain in which the nucleus is situated is intimately concerned with posture. This is an attractive hypothesis, particularly since it need not be an exclusive one.

Sixth hypothesis: The accessory optic system is concerned with circadian, estrus, and other rhythms. There is no good direct evidence for or against this hypothesis; as yet, earlier work on the ferret is inconclusive, and more recent investigation is unspecific.

As indicative of its autonomic character, the nucleus is situated in the midst of structures of the limbic system: the mammillary peduncle and the lateral mamillary nucleus on the medial side, the substantia nigra laterally, and the red nucleus dorsally. The passage of photic information via the accessory optic system to the limbic system seems probable.

Seventh hypothesis: The accessory optic system provides centrifugal control of the retina. This was the hypothesis which originated this project.[6] Because of the discovered polarity of the pathway, it was evident from almost the beginning that the nucleus of the transpeduncular tract could not be a centrifugal center for central control of retinal function. However, the accessory optic nucleus (or nucleus of the posterior accessory optic tract) could play a centrifugal role in addition to its centripetal one.

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Discussion of the Paper

SHAUL FELDMAN: Have you seen in your section any projections to the anterior regions like the hypothalamus; have you anything to confirm Knocke, and further have you recorded any latencies on this anterior region? I can confirm your latencies in the midbrain because in the cat one can record latencies of 40 or 50 milliseconds. I think Harmon and Berry have reported the same latencies in the cat midbrain. I wonder if you had anything more?

ELWIN MARG (*University of California, Berkeley, Calif.*): Our histological investigations in the rabbit show we have not been able to find any direct connections with the hypothalamus or with structures leading to the hypothalamus as yet, nor have we been able to find any direct connections from the optic chiasma to the hypothalamic area. As for latencies, our shortest latency was in the neighborhood of 20 milliseconds at the nucleus of the transpeduncular tract, this would be at the base of the midbrain.

No, we have done no recording from the hypothalamus.

J. BENOIT: I would like to make just a comment concerning the optical projections to the hypothalamus in the rabbit, on the basis of results obtained by three workers from my laboratory, Kordon, Gogan and Crandall, with the assistance of Buser for the neurophysiological part of the work.

They investigated responses to light under nembutal and chloralose anesthesia, in the medial and lateral parts of the preoptic and tuberal regions of the hypothalamus, and mapped the occurrence and the latency of responses in various experimental conditions. The preliminary conclusions are: (1) short latency responses have been observed in various parts of the hypothalamus, the most important ones being recorded in the medial and lateral regions; (2) the short latency responses in the hypothalamus are slower than the first geniculate response to vision, thus they could be either mediated by the geniculate nucleus or transmitted by slower fibers than the visual projections; and (3) two responses are usually present in the hypothalamus, short ones and slower and longer responses; the long responses may be evoked by geniculate nucleus or cortical stimulation. They seem to disappear after anesthesia of the primary visual cortex.

ELWIN MARG: I just wish to say that we are not endocrine people; we are vision people, and we realize that there is an endocrine system, but we really haven't gotten to it. Our point here is to establish that the accessory optic system is a direct pathway to the mesencephalon and that it should not be overlooked in considering the possible pathways of photic stimulation to the brain.