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City University of New York PH.D. 1981

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ELECTROPHYSIOLOGICAL CHARACTERISTICS OF OPTIC NERVE INPUT TO LATERAL ACCESSORY OPTIC NUCLEUS AND OTHER SUBCORTICAL STRUCTURES

by

DAVID PASSIKOFF

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1981

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Introduction

Anatomical studies have indicated for a long time that optic nerve (ON) fibers project to a variety of subcortical areas, such as the dorsal lateral geniculate nucleus (LGN), the superior colliculus (SC) and the pretectum (PRT) (see Polyak [1957] for history). Classically, electrophysiological studies have sought to differentiate nerve fibers on the basis of conduction velocity (Erlanger and Gasser, 1937). It is possible that ON fibers which differ in their terminations also differ in conduction velocity and other physiological characteristics. In 1955, Bishop and Clare pursued this possibility by applying a shock stimulus to the ON of the cat and recording from the dorsal and ventral parts of the LGN (layers A and A1 and B respectively), the SC and PRT. They defined four functional fiber groups in the ON on the basis of differences in threshold, amplitude and latency of response. They attributed these groups to projections to the SC, PRT, layers A and A1 and layer B of the LGN. When response latencies were converted to conduction velocities, they found values of 40-50 m/sec for layers A and A1, 15-25 m/sec for layer B, 6 m/sec for the PRT and 3.5 m/sec for SC. Threshold of response and response amplitude paralleled the conduction velocities, with threshold increasing and amplitude decreasing in going from layers A and A1 to layer B to the PRT and to the SC. However, Bishop and Clare (1955) did not study the ON fibers which terminate in other subcortical areas, such as the hypothalamus and the three accessory optic nuclei. Of these, the lateral accessory optic nucleus (LAON) was the main concern of the present work.

The results of some more recent studies do not agree with those of Bishop and Clare (1955) (see Table IA). Most of the differences in conduction velocities of the ON fibers innervating layers A and A1 seen in Table IA can be accounted for by different estimates of conduction distance. There is, however, general agreement on the value of the latency of response of layers A and A1 to ON stimulation (about .6-1.0 msec).

Estimates of the conduction distance of ON fibers to the SC have varied even more widely (see Table IB). Even where estimates of conduction distance have not varied much in some studies, differences in the conduction velocity of ON fibers to the SC have still been reported, due to vast differences in the latency of response to ON stimulation (see Table IB). The SC latency to ON stimulation can be grouped into two categories. There has been recorded a "slow" response (latency of about 6-11 msec) and a "fast" response (latency of about .8-2.0 msec) (see Table IB). The possibility that the "slow" response is relayed through the visual cortex (VC) can be eliminated, since Hoffmann (1972, 1973) obtained this response in decorticate cats.

In recent years, three types of retinal ganglion cells, X, Y and W cells, which have been defined mainly in terms of their receptive field characteristics, have been found to be distinguishable based on the conduction velocity of their axons. X cells are sometimes called tonic cells, since they respond continuously with no decrease in response to the presence of light. Y cells are sometimes called phasic cells, since they respond optimally to the onset and offset of light. Less is known of W cells. The axons of X cells conduct at 15-23 m/sec (Fukada, 1971), those of the Y cells at 30-40

Table I. Conduction velocities and conduction distances of cat ON fibers which innervate layers A and A1 of the LGN and SC. (Values listed are ranges, means or medians. The table is not exhaustive.)

A.	Study	Latency (msec)	Conduction Distance (mm)	Conduction Velocity (m/sec)
Layers A and A1 of LGN	Bishop and Clare (1955)	.6	22-25	40-50
	Vastola (1961)	.7-.8	43	54-62
	Dodt (1956)	*	*	70
	Fukada et al (1966)	*	37	30
B.				
"Fast" SC	Meulders et al (1963)	.8-1.4	30	30
	Marchiafava et al (1966)	1.1	60	54
	Hoffmann (1973)	1.2	50	40
	Hoffmann and Stone (1973)	*	*	35-45
"Slow" SC	Hoffmann (1973)	6	50	5.5
	Hoffmann and Stone (1973)	6	*	15
	Bishop and Clare (1955)	9-11	35	3.5
	Stone and Fukada (1974)	4.5-16	53	2.2-18
	Altman and Malis (1962)	7-9	40	5

* - Information unavailable

m/sec (Fukada, 1971) and those of the W cells at 2-18 m/sec (Stone and Hoffmann, 1972). The axons of the X and Y cells project to layers A, A1 and B of the LGN (Wilson et al, 1976). Y cell axons also project to the SC (Hoffmann, 1973). W cells send their axons to the SC (Hoffmann, 1973) and to layer B of the LGN (Cleland et al, 1976). Thus, it is possible that X, Y and W retinal ganglion cells are the sources of three functionally different groups of ON fibers, which have different central terminations.

There has, however, been little research on the conduction velocities of the ON fibers that innervate such structures as the PRT, pulvinar (PUL) and the LAON. It was the main purpose of the present study to obtain such information for the LAON and to compare it with that of the other subcortical visual nuclei.

While Bishop and Clare (1955) did record from the PRT, Clare et al (1969) suggested that the PRT electrode of Bishop and Clare (1955) was really in the SC. As far as the PUL is concerned, whether or not it even receives a direct retinal projection in the cat is still controversial. Based on anatomical studies, some (Minkowski, 1920) conclude that it does receive such a projection, while others (Barris et al, 1935) conclude that it does not. Based on electrophysiology, Bishop and Clare (1955) felt that their functional fiber group of the ON which went to layer B of the LGN was the source of ON innervation of the PUL, but they could not rule out the possibility of an intervening synapse in layer B. In fact, Altman (1962) found projections from all three layers of the LGN of the cat to PUL. On the other hand, Chalupa et al (1972) offered evidence, based on the use of cryogenic cooling of layer B, that PUL may receive

a direct projection from the retina. An ancillary purpose of the present study was to examine the question of whether or not the PUL receives a direct retinal projection.

The accessory optic system has received even less attention than has either the PRT or PUL, regarding the nature of its retinal input. The first modern description of the complete mammalian accessory optic system was made by Hayhow (1959) in the cat. The lateral accessory optic nucleus (LAON) was of major concern in the present inverstigation. The LAON receives crossed and uncrossed retinal input (Laties and Sprague, 1966) by way of the superior fasciculus of the accessory optic tract, which, at first, stays within the body of the main optic tract. At the anterior level of the SC, the superior fasciculus branches off from the brachium of the superior fasciculus (BSC) and turns downward. Some of its axons immediately terminate in the dorsal accessory optic nucleus (DAON). Most of the fibers of the superior fasciculus continue past the DAON, and traverse the medial geniculate nucleus (MGN) dorsoventrally to terminate in the LAON, lying just ventral to the medial part of the posterior aspect of the MGN and just dorsal to the cerebral peduncle. Anteriorly, the LAON lies more ventrally, even being located under the cerebral peduncle at the most anterior extent of the nucleus.

There is very little anatomical information on the fiber connections of the cat LAON. It has been found to receive projections from striate cortex (Garey et al, 1968) and from the ventral lateral geniculate nucleus (Swanson et al, 1974). Almost nothing is known about the fiber group(s) of the ON that innervate(s) the LAON. Based on electrophysiology, Kozak (1971) found the response of the

cat LAON to light to be as fast as, or faster than, that of the the LGN. He reported a conduction velocity for the ON fibers that innervate the cat LAON of 15-23 m/sec. There is no published anatomical information on the projections of the cat LAON. The present study attempted to explore the question of which subcortical visual structures send fibers to, and/or receive fibers from, the LAON of the cat.

There is also very little information on the behavioral significance of the LAON. Marg (1964) suggested that the whole accessory optic system might mediate photic activation of the brainstem reticular formation, while Maekawa and Simpson (1973) suggested that various parts of the accessory optic system mediate visual input to the vestibulocerebellum in the rabbit. In the rhesus monkey, the Pasiks (T.Pasik and P.Pasik, 1971, 1973) have shown that removing, bilaterally, striate cortex, parts of areas 18 and 19, the LGN, PUL and medial PRT leaves the animal still able to discriminate between the presence and absence of light. However, an additional bilateral lesion of the LAON rendered such an animal unable to make this discrimination. In fact, bilateral lesions of just visual cortex and the LAON were sufficient to produce this apparent blindness. But, bilateral lesions of just the LAON produced no noticeable behavioral deficit.

Several sources of error were eliminated in the present study by using a shock stimulus applied directly to the ON to investigate the conduction velocities and other characteristics of the ON fibers. For example, it will be recalled that Kozak (1971) recorded the response of the LAON to a light stimulus which was, therefore, subject to temporal and spatial dispersion within the retina. The conduction velocity which he gives includes conduction velocity within the

retina, which is much slower than the extraretinal conduction velocity of ON fibers (Dodt, 1956; Rowe and Stone, 1976) and artificially reduces the conduction velocity of the ON fibers which innervate the LAON. This source of error was eliminated in the present study by applying an electrical stimulus directly to the ON, after the eye had been removed. The removal of the eye also facilitates the interpretation of responses recorded from the ON upon stimulation of central visual structures. That is, if efferents do course through the ON (see below), then if the eye were not removed, stimulation of a central visual structure might produce, in the records from the ON, complex responses representing antidromic, orthodromic and postsynaptic activity. This would make the interpretation of such activity considerably more complicated. So, for this reason too, the eye was removed in the present study.

The present study sought to determine the conduction velocity, threshold and amplitude of response of the ON fibers innervating the LAON and to compare these with those of several other subcortical structures (layers A and A1 and layer B of the LGN, SC, PRT and PUL). Secondarily, it attempted to determine which of these structures (as well as the ON and mesencephalic reticular formation [MRF]) send projections to, and/or receive projections from, the LAON. Thus, in almost every cat used in the present study, dual purpose stimulating and recording electrodes were placed in the ON, LAON, LGN, SC, PRT, PUL and MRF.

With a stimulating/recording electrode on the ON, and one in each subcortical visual structure, one is in a favorable position to investigate the existence of centrifugal fibers originating in any

of these structures and terminating in the retina. All that is required is to dissociate orthodromic from antidromic responses on the basis of latency and waveform. The criteria which were used to make this dissociation in the present study will be listed in the Method section. The possibility of centrifugal fibers in the ON has been a controversial subject for many years. There is general agreement that such centrifugal fibers do exist in birds (Cowan et al, 1961; Miles, 1970, 1971). In the cat, however, evidence for the existence of such fibers has been given by some (Fillenz and Glees, 1961; Gorikov, 1969), but not by others (Brindley and Hamasaki, 1966; Lin and Ingram, 1973). Part of the present study sought to investigate the possibility of centrifugal fibers in the ON of the cat, with special emphasis on the LAON as their source.

In summary, the main purpose of the present study was to investigate the nature of the functional fiber group(s) of the ON which innervate(s) the LAON and to compare this with that of those that innervate the other subcortical visual structures. Secondarily, the present study sought to explore the question of which subcortical visual structures send fibers to, and/or receive fibers from, the LAON. Finally, the present study attempted to determine, electrophysiologically, if centrifugal fibers coursing through the ON exist in the cat, and if so, to locate their source, with special attention to the LAON. To accomplish these purposes, cats were acutely prepared with stimulating/recording electrodes in the ON, LAON, LGN, SC, PRT, PUL and MRF.

Method

Subjects

Data were collected from 35 adult cats (Felis domesticus), weighing between 2.0 and 6.0 kg. The animals were food-deprived for 24 hours prior to the beginning of each experiment.

Anesthesia

All animals were anesthetized by intraperitoneal injections of sodium pentobarbital (Nembutal, Abbott Laboratories, 50 mg/ml, 33 mg/kg). For some animals, supplements of .2 to .5 cc were required to obtain a surgical level of anesthesia.

Throughout the course of each experiment, the animals were maintained at a light-to-moderate level of anesthesia. The criteria to judge level of anesthesia were the relative briskness of response to pain (a hemostat clamped to the toe pad) and the relative briskness of the corneal response. Intravenous supplements of .2 to .3 cc of Nembutal were given, as needed, throughout each experiment, to maintain this light-to-moderate level of anesthesia.

At the end of each experiment, the animal was sacrificed by an intravenous injection of from 2.5 to 10 cc of Nembutal.

Surgery

The trachea was exposed via a midline incision in the neck area,

followed by a separation of tissue overlying the trachea. The exposed trachea was cut transversely, and a canula was inserted and tied tightly to the trachea with surgical thread. Adhesive tape was wound around the neck to help keep the tracheal canula in place. Tracheal cannulation was for the purpose of artificially respirating the animal with a respiration pump (Harvard Apparatus, Model 607) if the animal stopped breathing during the course of the experiment. All other surgery was performed with the animal's head in a stereotaxic instrument.

The left optic nerve was exposed and a suture was tied around the optic nerve at the point where it exits the eye. The eye was collapsed and removed, except that a stump of sclera, no greater in size than 2 square mm, was left attached to the optic nerve. The retina was scraped away. Much of the tissue in the orbit was removed, so that about 10 to 15 mm of the nerve was clearly visible. Finally, the dura was carefully dissected from the optic nerve for a distance of 5 to 10 mm from its exit from the back of the eye.

Cranial surgery consisted of a midline incision, followed by removal of fascia and reflection of the temporal muscles. A craniectomy on the right side exposed the cranial contents from approximately 10 mm anterior to the interaural line to the tentorial covering of the cerebellum, and from the midline laterally for 15 mm. The exposed dura was incised and reflected.

The skin of the lower left hind limb was incised, exposing the saphenous vein, which was cannulated with a hypodermic needle attached to thin plastic tubing.

Animal Maintenance

Each animal was given intravenously a 5 percent solution of dextrose in normal saline (Abbott Laboratories) throughout the course of each experiment, at about 1 drop/lb/min (60 drops/cc).

Every 2 to 3 hours, a local anesthetic, propitocaine (Citanest, Astra Pharmaceutical Products), was liberally infused into all wounds and pressure points, except directly into the exposed orbit.

Warm physiological saline was frequently applied to the exposed cortex, and less frequently applied to the exposed optic nerve (see General Procedure below).

Stereotaxis

Each animal was mounted in a standard cat stereotaxic instrument (David Kopf Instruments). Bipolar electrodes were directed into the LGN, PUL, SC, PRT and MRF, all on the right side. Coordinates for these structures were obtained from Jasper and Ajmone-Marsan (1954).

One SC-MRF electrode was used to stimulate and record from both the SC and MRF, by lowering it to the appropriate H value. The SC-MRF and PRT electrodes were mounted on the same electrode carrier. The LGN and PUL electrodes were mounted on one other electrode carrier.

Four electrodes, all mounted on a third electrode carrier, each 1 mm from its neighbor, were calibrated for placement in the right LAON, according to the stereotaxic atlas of Berman (1968). Four electrodes were used in order to increase the liklihood that at least

one of these electrodes would arrive at the LAON, since the LAON is quite small (about 1 cubic mm), especially in relation to the rest of the brain.

Electrodes

All electrodes used in the present study were bipolar. The four electrodes destined for the LAON were concentric, and each consisted of a 0.005 inch tungsten wire, insulated with formvar, except for the flush-cut tip, inserted into a 24 guage stainless steel hypodermic tubing, also insulated, except at the concentric tip. The inner electrode tip extended 1 mm from the edge of its tube.

The electrodes destined for the SC-MRF, PRT, LGN and PUL each consisted of two pieces of 0.010 inch tungsten wire, each insulated with formvar, except for the flush-cut tip, and encased in a 20 guage stainless steel tube, also formvar insulated. The tips extended 1 mm beyond the edge of the tube, and were separated from each other by about .5 mm.

The electrode used to stimulate and record from the ON was fashioned out of two silver wires, the uninsulated tips of which were housed in the bottom half of a small plastic clip. The tips of the two wires were fixed in a semicircular position, and were parallel to each other, separated by 2 mm. Each uninsulated tip extended out onto the inside surface of the lower half of the clip for about 5 mm. The clip was constructed with a very low tension spring, which would gently close the top of the clip over the bottom. The shape of the upper and lower halves of the clip allowed for the

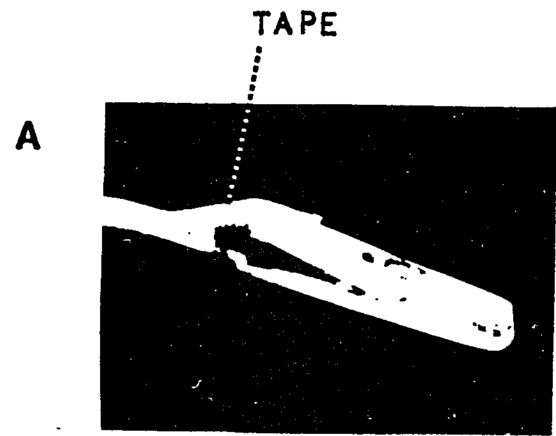
placement of a small cylindrical object (the ON) between them. When this electrode was clipped onto the ON, it was held in place by the slight downward pressure of the upper half of the clip. The two uninsulated tips of the electrode were each in contact with the ON over approximately half of its circumference. The ON electrode is shown in Figure 1.

Stimulation and Recording Equipment

Every 8 seconds, a waveform generator (Tektronix Type 162) triggered a second waveform generator (Tektronix Type 162). This second waveform generator provided a time base for a pulse generator (Tektronix Type 161). This pulse generator gated on a stimulator (Grass S-44), the output of which was fed to the ON, SC-MRF, LGN or PUL electrode, by way of a stimulus isolation unit (Grass Model SIU-5A), or, was fed, also by way of the stimulus isolation unit, to a double-pole selector switch (with four positions), which was used to select one of the four LAON electrodes for stimulation. The onset of this gate triggered the time base of a split beam oscilloscope (Tektronix Type 561A).

Recorded activity was fed, by way of a cathode follower (Grass HI Z Probe Model HIP511E) (or, first, to the selector switch, if from an LAON electrode), to a differential AC preamplifier (Grass Model P511C; -3 db at 10 Hz to 10 KHz), and was displayed on the bottom channel of the oscilloscope. The top channel of the oscilloscope was used to display the amplitude of the monitored stimulating current, by way of input from an inductively coupled current probe

Figure 1. The optic nerve electrode used in the present study. A. Photograph of the ON electrode, with the clip held open with tape. Magnification: about X 2. B. Schematic diagram of the ON electrode, with the clip open.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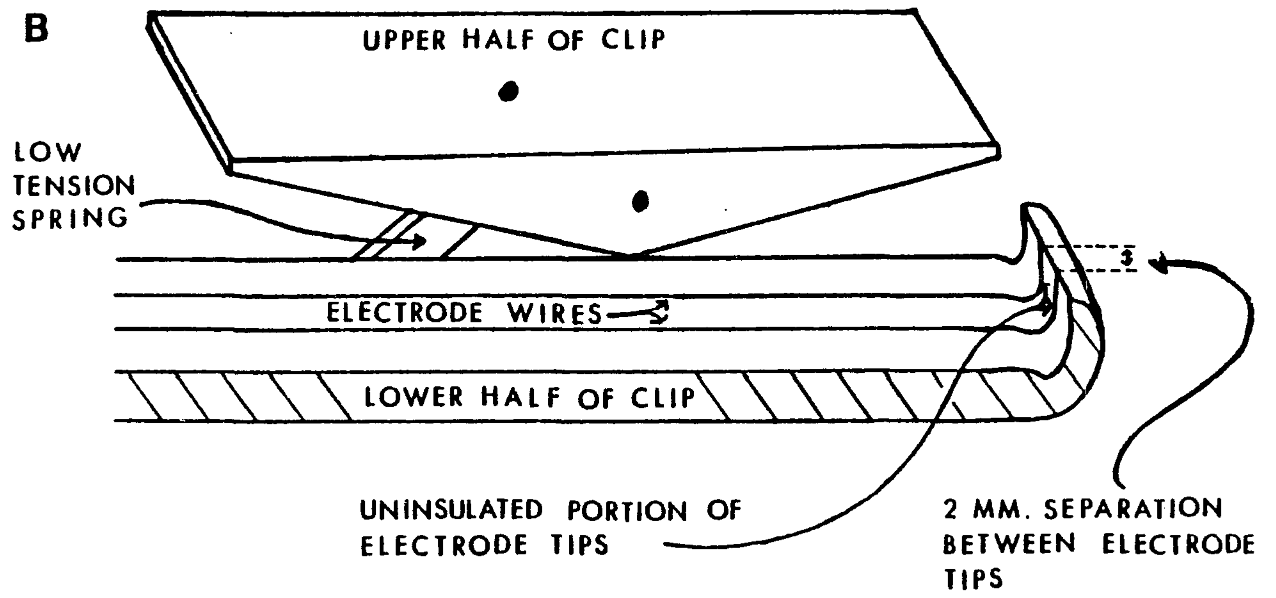
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ELECTRODE WIRES
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ELECTRODE TIPS
2 MM. SEPARATION
BETWEEN ELECTRODE
TIPS

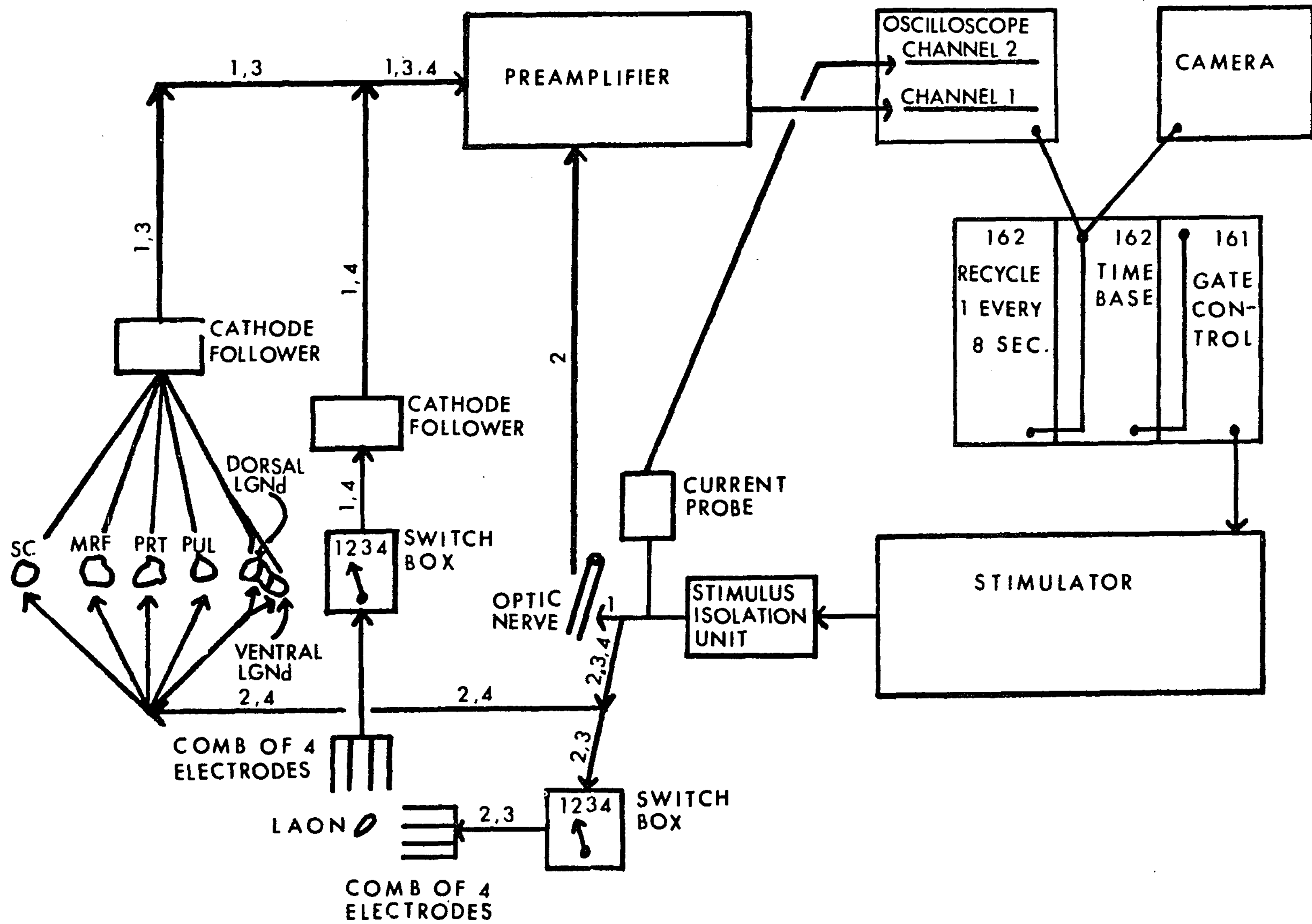
(Tektronix Type 134) clipped onto the positive lead coming from the stimulus isolation unit to the stimulating electrode.

A camera (Grass Kymograph C4-J) was used to photograph recorded activity as it was displayed on the oscilloscope. When this was done, a pulse from the camera triggered the second waveform generator, instead of the first waveform generator doing so. Figure 2 is a schematic diagram of the stimulating and recording equipment used.

Histology

After each animal was sacrificed and the brain was exposed, the head was removed and placed in a 10 percent solution of formalin for a minimum of 7 days. The head was then remounted in the stereotaxic instrument, and a block of brain tissue, from approximately A 23.0 to P 13.0 was cut, in the coronal plane, by the use of a no. 20 scalpel blade mounted on an electrode carrier. This block of brain tissue was then placed in a 10 percent solution of formalin for a minimum of 10 days. Each such block of tissue was then processed by the frozen section technique. Coronal sections 48 um thick were cut from just anterior to the optic chiasm to just posterior to the superior colliculus. Every fifth section was saved through the marking lesions, except in the region of the four tracks of the LAON electrodes, where every third section was saved. Otherwise, every tenth section was saved. Sections were stained by the method of Klüver and Barrera (1953).

Figure 2. Schematic diagram of the arrangement of the stimulating and recording equipment used in the present study. Four differnt partially overlapping "pathways" of stimulation and recording are depicted by labelling the parts of each pathway with the numbers 1, 2, 3 and 4, respectively. Thus, pathway 1 is arranged for stimulation of the ON and recording of activity from the LAON, LGN, SC, PRT, PUL and MRF, one at a time. Pathway 2 is arranged for stimulation of the LAON, LGN, SC, PRT, PUL and MRF, one at a time, and recording of activity from the ON. Pathway 3 allows for stimulation of the LAON and recording of activity from the LGN, SC, PRT, PUL and MRF, one at a time. Pathway 4 allows for stimulation of the LGN, SC, PRT, PUL and MRF, one at a time, and recording of activity from the LAON. Parts of the diagram which are not labelled with numbers are used in all four pathways.


PREAMPLIFIER
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2,4
2,3,4
COMB OF 4
ELECTRODES
2,3
LAON
2,3
1234
SWITCH
BOX
COMB OF 4
ELECTRODES

General Procedure

The sequence of events in each experiment was as follows. Following anesthesia and tracheal cannulation, the animal was placed in the stereotaxic instrument. The saphenous vein was cannulated and the drip was started. The optic nerve was exposed, the craniectomy was performed and the ON electrode was applied to the ON, such that an edge of the plastic clip housing the electrode was pressed up against the stump of sclera. Thus, the effective site of stimulation was at the exit of the ON from the back of the eye, the very beginning of the extra-ophthalmic portion of the ON. The LAON electrodes were directed to their predetermined coordinates and stimulation of the ON began. The recycling rate for all conditions of stimulation was 8.0 seconds.

For all stimulation and recording in the present study, stimulus energies ranged from 500 nanocoulombs down to threshold, in approximately 50 or 100 nanocoulomb steps. However, when thresholds were lower than 50 nanocoulombs, 25, 10, 5, 2 and 1 nanocoulomb steps were used. Every response at each stimulus energy level, as displayed on the oscilloscope, was photographed, and, in addition, one photograph of five superimposed sweeps was taken for every stimulation-recording condition, usually with a high stimulus energy level. Stimulus duration was .5 msec, except in some conditions in five to eight animals, where it varied from .3 msec to .05 msec.

After recording from the LAON, stimulation and recording were reversed and recordings were taken from the ON following LAON stimulation. Then, the SC-MRF and PRT electrodes were inserted and recor-

dings were taken from the SC and PRT to ON stimulation and vice versa. The SC-MRF electrode was then further lowered into the MRF. Records were taken from the MRF upon ON and LAON stimulation, and vice versa. The LGN and PUL electrodes were then lowered into the brain, and records were taken from the LGN and PUL upon ON and LAON stimulation, and vice versa. In five animals, the LGN electrode was further lowered to layer B and the procedure was repeated. In the first four animals studied, stimulation of, and recording from, the MRF, LGN and PUL did not take place.

Saline evaporated very slowly from the exposed portion of the optic nerve, and even more slowly from the part of the optic nerve enclosed by the plastic clip housing the ON electrode. Thus, application of warm physiological saline to the exposed portion of the optic nerve was needed less frequently than it was to cortex, and therefore, the ON enclosed by the clip was irrigated about once every 3 hours. When such application was required, the saline was carefully applied to the ON in individual drops.

Upon sacrifice of the animal, marking lesions to indicate the locus of subcortical electrode tips were produced by anodal fulgaration of 10 to 30 sec duration and .1 to .4 milliamperes of current.

In the case of the four LAON electrodes, sometimes the electrode tip furthest from the electrode tip which yielded the best responses was used for marking. This was done to avoid risking the possibility of destroying the actual site of optimal stimulation and recording, since the LAON is of such a small size. When this was done, the distance between the electrode from which the best responses (defined by clarity and amplitude of components) were recorded and

that used for marking, was noted. The entire exposed optic nerve was dissected free from all surrounding tissue, up to its entrance to the optic chiasm (OX), and was removed. The animal was decapitated to prepare the brain for histological treatment.

Measurement of Length of ON-OT

At the end of each experiment, after the animal had been sacrificed, the exposed optic nerve was transected at its entrance to the OX, and its length was measured by placing it along a mm rule. In addition, three normal cats were sacrificed and their brains and left optic nerves were exposed, and removed intact, after the eyes were severed from the ONs at the exit of the ON from the eye. Each optic nerve was measured by placing a piece of surgical thread along its length, up to its entrance to the chiasm, and then measuring the length of the thread. The three brains were then placed in a 10 percent solution of formalin, for a minimum of 10 days, so that they would be firm enough for dissection. Each of these three brains was then carefully dissected, so as to expose the optic tract up to its entrance into the ventral part of the LGN, and beyond. In all three cases, it was possible to follow the OT only up to a point approximately 5 mm past its entrance to the ventral part of the LGN. A piece of surgical thread was placed on top of the ON-OT up to its entrance into the ventral part of the contralateral LGN and was then measured. The same procedure was followed to measure the length of the OT up to its entrance into the OX. These procedures were followed for all three of these brains. Since the length of the

fresh normal ON up to its entrance into the OX was known in all three cases, it was possible to calculate the degree to which formalin had changed this length. This shrinkage factor could then be applied to the lengths found for the OT in the formalinized brains.

The length of the ON-OT up to its entrance to the ventral part of the LGN could, thus, be determined. In order to determine a minimum length of the ON-OT into the SC, PRT and LAON, the Pythagorean theorem was applied to the plates presented in a number of stereotaxic atlases of the cat brain (Berman, 1968; Jasper and Ajmone-Marsan, 1954; Snider and Niemer, 1961; Fifkova and Marsala, 1967). The details of the application of this method can be found in Appendix 1.

Analyaia of Data

The amplitude and latency of each component of each response to each level of stimulation was measured from the film taken during each experiment. The threshold stimulation energy of every component of all responses was also determined. Median amplitude values of each component of most responses were plotted as a function of stimulus energy. Median threshold and latency values for every component of all responses at each level of stimulus energy were also computed. Conduction velocities (in meters/second [m/sec]) were computed by dividing the median latency value obtained for a given component of the response of a given structure, into the determined length of the ON-OT to that structure.

In order to determine whether the individual components of the

responses represented presynaptic or postsynaptic, orthodromic or antidromic, centrifugal or centripetal activity, several interlocking neurophysiological principles were applied to the analysis of the responses. Briefly, the principles used were (1) the existence of a synaptic delay of a few tenths of a msec, (2) the fact that an antidromic response cannot cross a synapse and (3) the fact that antidromic conduction velocity is the same as orthodromic conduction velocity. A detailed example of the kind of analysis which was undertaken is presented in Appendix 2.

Results

I. Length of ON-OT

The median length of the fresh ON from its exit from the eye to its entrance into the OX was measured to be 18 mm (range: 17-20 mm). Table II presents the estimated length of the OT from the most anterior aspect of the OX to the entrance of the OT into the ventral-most part of the LGN. The median estimated length of the OT from its entrance into the OX to its entrance into the most ventral part of the LGN (the median of the three values presented in the bottom row of Table II) was 18 mm (rounding off to the nearest .5 mm). This value of 18 mm, when added to the already obtained median value of 18 mm for the length of the ON from its exit from the eye to its entrance into the OX, yields an estimate of 36 mm as the distance traversed by the ON-OT in going from the eye to the most ventral part of the LGN.

The estimated minimum distances traversed by the OT fibers in going to the PRT, SC and LAON from the point of their departure from the OT fibers entering layer B of the LGN, as well as the estimated minimum distance traversed by the OT fibers in going from the point of their entrance into layer B to the more dorsal layers, based on the atlases of Berman (1968), Fifkova and Marsala (1967), Jasper and Ajmone-Marsan (1954) and Snider and Niemer (1961), are presented in Table III. In order to obtain an estimated minimum length of the ON-OT into the PRT, SC and LAON (but not the dorsal part of the LGN), 1 mm was subtracted from the already obtained

Table II. Estimate of the length of the fresh OT from the anteriormost OX to the entrance of the OT fibers into layer B of the LGN, and data upon which these estimates were based. In each of the three cats, the correction factor was applied to the formalinized length of the OT. All lengths, measured and estimated, are rounded off to the nearest .5 mm.

		Cats		
		1	2	3
Length (in mm) of ON from its exit from eye to its entrance into the OX	Fresh	18.0	18.0	19.0
	Formalinized	17.0	16.5	18.0
Difference between fresh and formalinized above	Absolute	1.0	1.5	1.0
	Percentage (Correction factor)	5.6	8.3	5.3
Length (in mm) of OT from anteriormost OX to entrance into ventralmost aspect of LGN	Formalinized	17.0	16.5	17.5
	Estimated fresh	18.0	18.0	18.5

Table III. Minimum distance (in mm) traversed by the OT fibers in going from the point where they branch off from those OT fibers entering the ventral part of the LGN to the approximate loci of stimulation and recording, in the present study, within the PRT, SC, and LAON, measured in the atlases listed. In addition, the minimum distance (in mm) traversed by the OT fibers in going from their entrance to layer B of the LGN to the approximate loci of stimulation and recording, in the present study, within the dorsal layers of the LGN, are also listed. Median values are rounded to nearest whole mm; all other values are rounded to nearest .1 mm.

	Distance from point of entrance of OT fibers into layer B of the LGN to layers A and A1 of the LGN, and distance from a point 1 mm below this point of entrance of OT fibers into layer B to PRT, SC and LAON			
Cat Brain Atlases	Layers A and A1 of LGN	PRT	SC	LAON
Snider and Niemer (1961)	2.5	9.3	10.2	15.9
Fifkova and Marsala (1967)	2.5	8.1	9.5	*
Berman (1968)	1.5	8.2	9.2	14.4
Jasper and Ajmone-Marsan (1954)	2.0	7.7	9.5	14.0
Median	2.0	8.0	10.0	14.0

* - Impossible to measure; see Method section for explanation.

value of 36 mm for the length of the ON-OT up to its entrance into layer B, to give a value of 35 mm, since those OT fibers entering the LGN are not the ones coursing medially just below the LGN, headed for their terminations in the PRT, SC and LAON. This value of 35 mm (36 mm in the case of the dorsal layers of the LGN, since the OT fibers entering layer B are the fibers which terminate in the dorsal layers) when added to the values given in the bottom row of Table III gives median minimum estimates of the distances traversed by the ON-OT in coursing to the dorsal layers of the LGN, PRT, SC and LAON of 38, 43, 45 and 49 mm respectively.

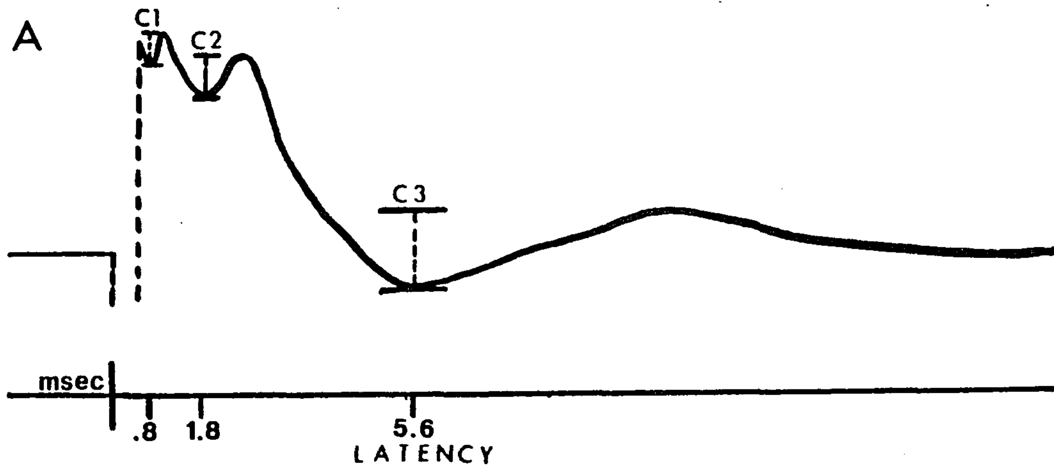
II. Optic nerve input to LAON

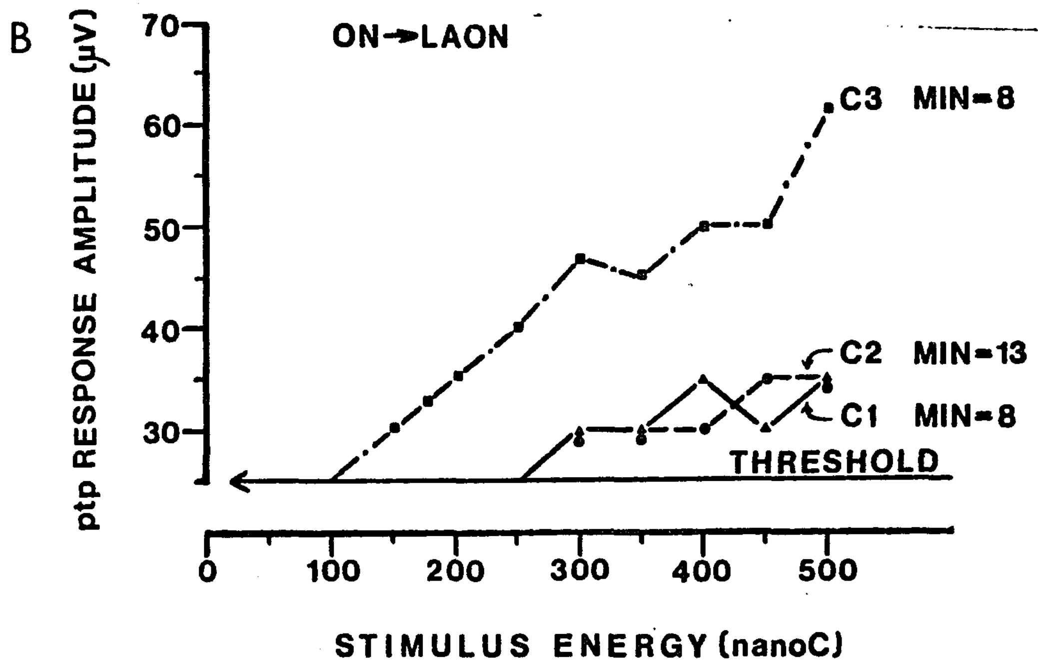
A. Response to ON stimulation

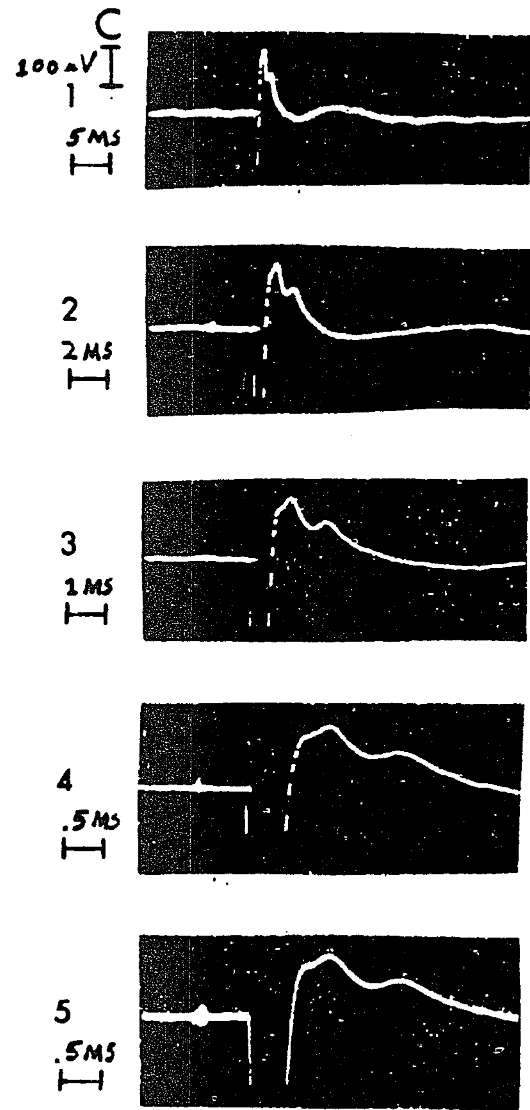
The response of the LAON to ON stimulation consists of three components. Figure 3A presents a schematic diagram of the response, and defines its three components. (See Appendix 3 for discussion of polarity in this and all other figures.) The median response latencies for the three components, C1, C2 and C3, are .8 (range: .6-.95), 1.8 (range: 1.6-1.9) and 5.6 (range: 5.5-5.7) msec respectively. The median threshold energies (defined throughout the present study as the amount of stimulus energy required to elicit a response of 25 uV) for the three components are 250, 250 and 100 nanoC respectively. Figure 3B presents the median response amplitudes of all three components of the LAON response to ON stimulation, as a function of stimulus energy.

In Figure 3C is presented a series of photographs of the LAON

Figure 3. Response of the LAON to ON stimulation. A. A schematic drawing of the typical response. Each component is labelled at, and median latency is given for, the first inflection of each component. The first thick dashed lines represent the onset and offset of the shock artifact. The other dashed lines define the amplitude of each component. B. Median peak to peak (ptp) amplitudes of each of the three components of the response, presented as a function of stimulus energy. MIN = the minimum number of animals used to obtain each point in a function. C. A series of photographs of one response, with different time bases. The amplitude marker given next to photo 1 applies to all others as well. Photo 5 is the same as photo 4, except that it depicts five superimposed sweeps. Note that with slow time bases (photos 1 and 2), it is hard to discern C1, but with faster time bases (photos 4 and 5), C3 is off the oscilloscope screen.


A
C1
C2
C3
msec
.8
1.8
5.6
LATENCY


B
ptp RESPONSE AMPLITUDE (μV)
70
60
50
40
30
ON→LAON
C3 MIN=8
C2 MIN=13
C1 MIN=8
THRESHOLD
0
100
200
300
400
500
STIMULUS ENERGY (nanoC)


C
100 μV
1
5 MS
2
2 MS
3
1 MS
4
.5 MS
5
.5 MS

response to ON stimulation with different time bases. Because of the very short latency of C1 and the long duration of the whole response, a time base slow enough to allow the depiction of all of C3 obscures C1 (Figure 3C, photo 1). Conversely, a time base fast enough to allow for good definition of C1 does not portray C3 on the oscilloscope screen (Figure 3C, photos 4 and 5).

The response sometimes consists of just C2 and C3. In Figure 4A is presented a series of photographs of the LAON response to ON stimulation, with a time base that allows for the depiction of C1 and C2, but not C3. It can be seen that C1 and C2 drop out of the response at the same time. Figure 4B presents a series of photographs with a slower time base, revealing just C2 and C3. It is to be noted that C3 remains after C2 has dropped out.

In four out of the 23 animals in which the LAON response to ON stimulation was recorded, the latencies of C1 and C2 were decidedly longer than in the other 19 animals, while that of C3 remained unchanged. The LAON data from these four animals were excluded from Figure 3B and from median latency calculations. The range of latencies of C1 in these four animals was from 1.1 to 1.6 msec, while that of C2 was from 2.1 to 2.6 msec. Figure 5 compares the LAON response of these four animals with that of the other 19 animals, and demonstrates the fact that C1 and C2 of the LAON response are time-locked.

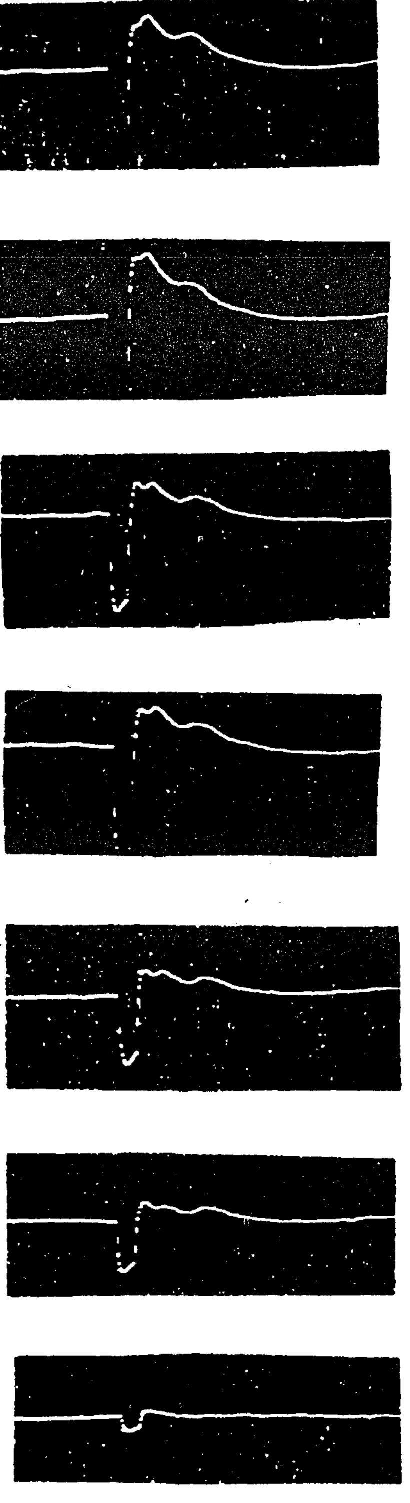
B. Optic nerve response

The response of the ON to LAON stimulation consists of three

Figure 4. Two series of photographs of the response of the LAON to decreasing stimulus energies applied to the ON. A. Fast time base, so that C1 can be discerned. B. Slow time base, so that C3 can be observed. Time and intensity markers given next to the first photos of A and B apply to all the photos in their respective series.

ON → LAON

A



B

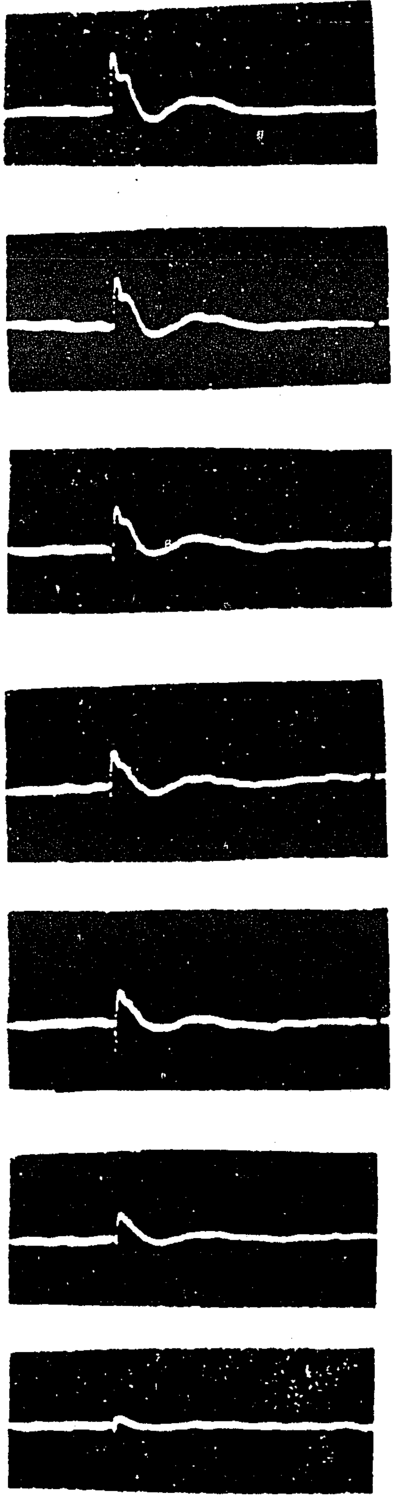
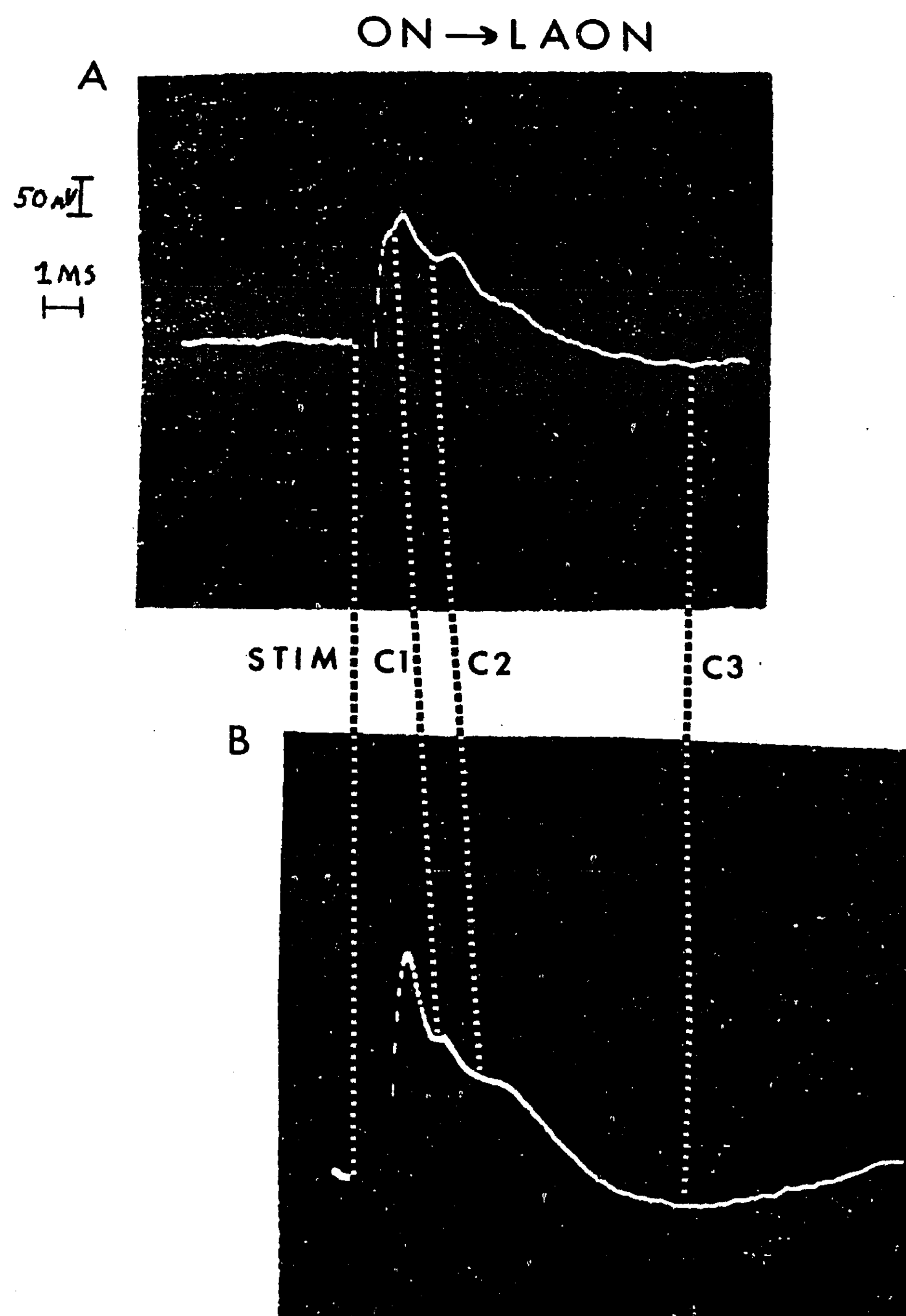


Figure 5. Demonstration of the fact that C1 and C2 of the LAON response to ON stimulation are time-locked. A. An LAON response to ON stimulation with short latency C1 and C2. B. An LAON response to ON stimulation from one of the four cats with longer latency C1 and C2. The line marked "STIM" connects the onset of the stimulus in A and B. The fact that the line connecting the two C3s is parallel to the "STIM" line indicates that the latency of C3 is the same in both A and B. The fact that the line connecting the two C1s and the line connecting the two C2s are not parallel to the "STIM" line (nor to the line connecting the two C3s) indicates that the two C1s have different latencies and that these two C2s have different latencies. The fact that the line connecting the two C1s is parallel to the line connecting the two C2s indicates that the difference in latency between C2 of A and C2 of B is exactly equal to the difrerence in latency between C1 of A and C1 of B. That is, C1 and C2 are time-locked. They vary in time together. Amplitude and time markers given next to A apply to B as well.


ON → LAON
A
50 μV
1 MS
STIM
C1
C2
C3
B

components. Figure 6 presents latency, amplitude and threshold data for the response, and defines its three components. The median response latencies for the three components are .8 (range: .7-1.0), 2.1 (range: 1.9-2.3) and 5.5 (range: 5.4-5.7) msec respectively. The median threshold energies for the three components are 200, 250 and 100 nanoC respectively. As can be seen in Figure 6A, B and C, C2, when present, has a much larger amplitude than C1 and C3. In addition, photos 3 and 4 of Figure 6C depict the sudden dropping out of C2, leaving just C1 and C3.

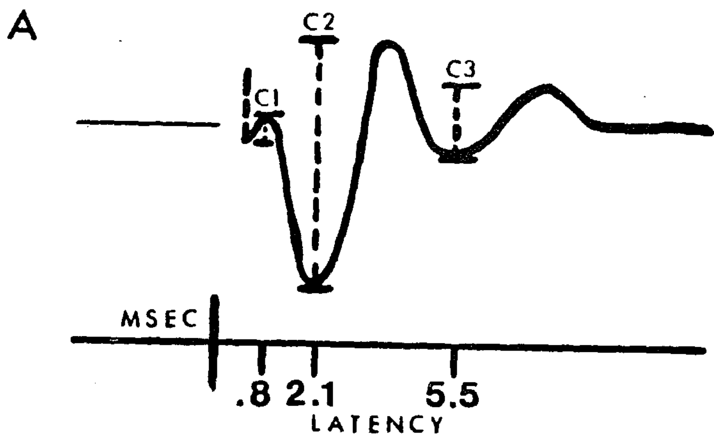
III. Optic nerve input to other subcortical visual nuclei

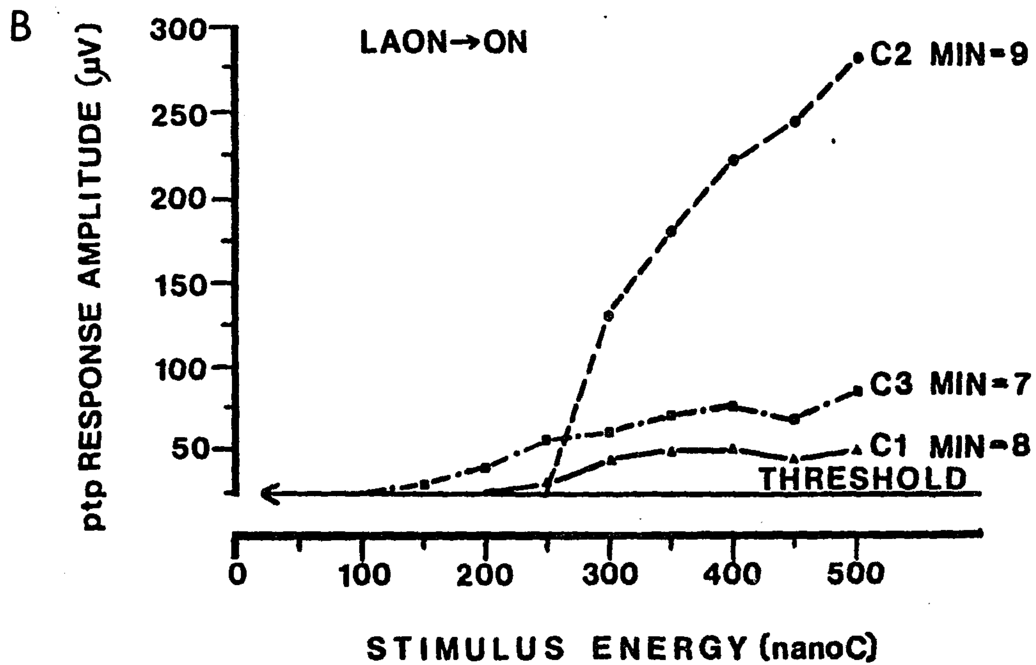
A. Layers A and A1 of LGN

1. Response to ON stimulation

The response of the dorsal layers of the LGN to ON stimulation consists of three components. Rarely, a long latency, low amplitude fourth component is present. Figure 7 presents latency, amplitude and threshold data for the response, and defines its three components. The median response latencies for the three components are 1.1 (range: .8-1.3), 2.0 (range: 1.7-2.5) and 2.5 (range: 2.2-3.1) msec respectively. The median threshold energies for the three components are 250, 50 and 40 nanoC respectively. Note that C1 in Figure 7C drops out before C2 and C3, and that C2 and C3 drop out in unison. In addition, Figure 8 demonstrates the fact that C2 and C3 are time-locked.

Figure 6. Response of the ON to LAON stimulation. A. A schematic drawing of the typical response. Labelling as in Figure 3A. B. Median peak to peak (ptp) amplitudes of each of the three components of the response, presented as a function of stimulus energy. Labelling as in Figure 3B. C. Series of photographs of the ON response to decreasing stimulus energies applied to the LAON. Time marker next to photo 1 applies to all other photos as well. Amplitude marker next to photo 1 applies to photos 2 and 3 as well. Amplitude marker next to photo 4 applies to photos 5, 6 and 7 as well.


A
C2
C1
C3
MSEC
.8 2.1 5.5
LATENCY


B
ptp RESPONSE AMPLITUDE (µV)
300
250
200
150
100
50
LAON→ON
C2 MIN=9
C3 MIN=7
C1 MIN=8
THRESHOLD
0
100
200
300
400
500
STIMULUS ENERGY (nanoC)

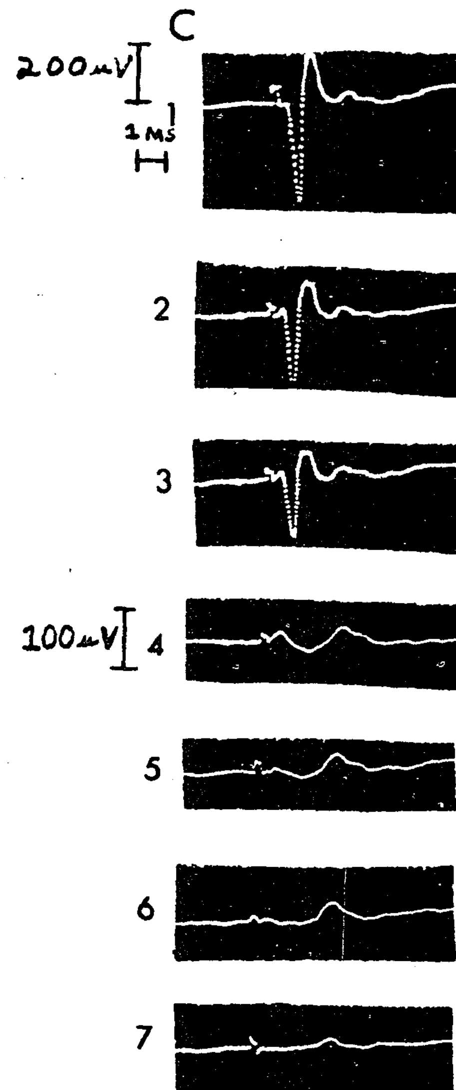
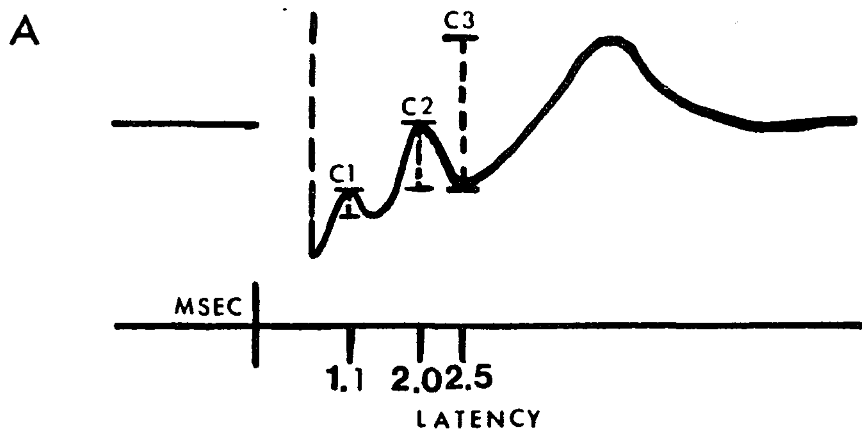
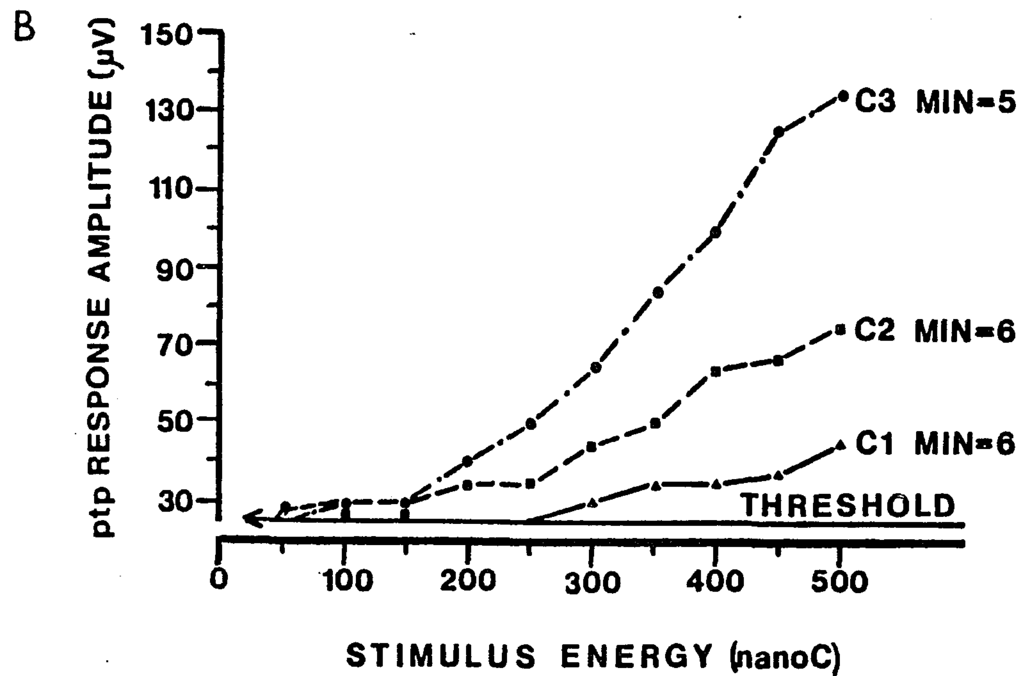

C
200µV
1 MS
2
3
100µV
4
5
6
7

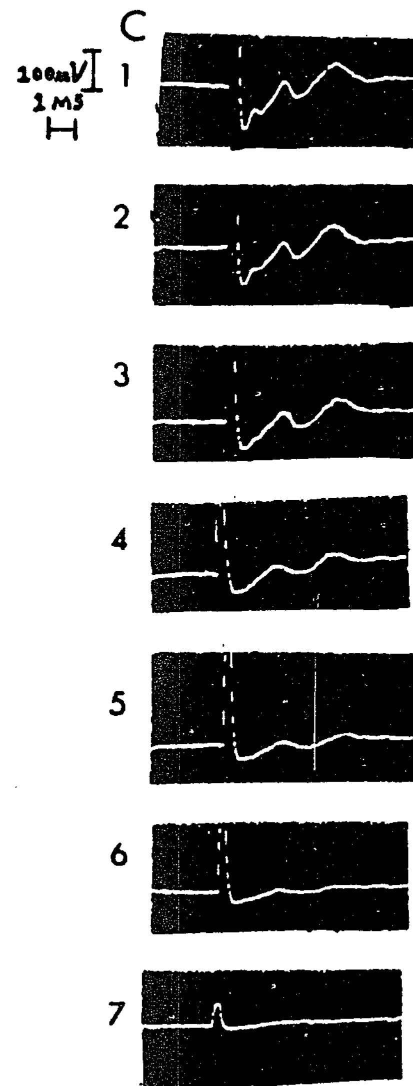
Figure 7. Response of layers A and Al of the LGN to stimulation of the ON. A. A schematic drawing of the typical response. Labelling as in Figure 3A. B. Median peak to peak (ptp) amplitude of each of the three components, presented as a function of stimulus energy. Labelling as in Figure 3B. C. Series of photographs of the response of the dorsal layers of the LGN to decreasing stimulus energies applied to the ON. Time and amplitude markers next to photo 1 apply to all other photos as well.



A
C1
C2
C3
MSEC
1.1
2.0
2.5
LATENCY

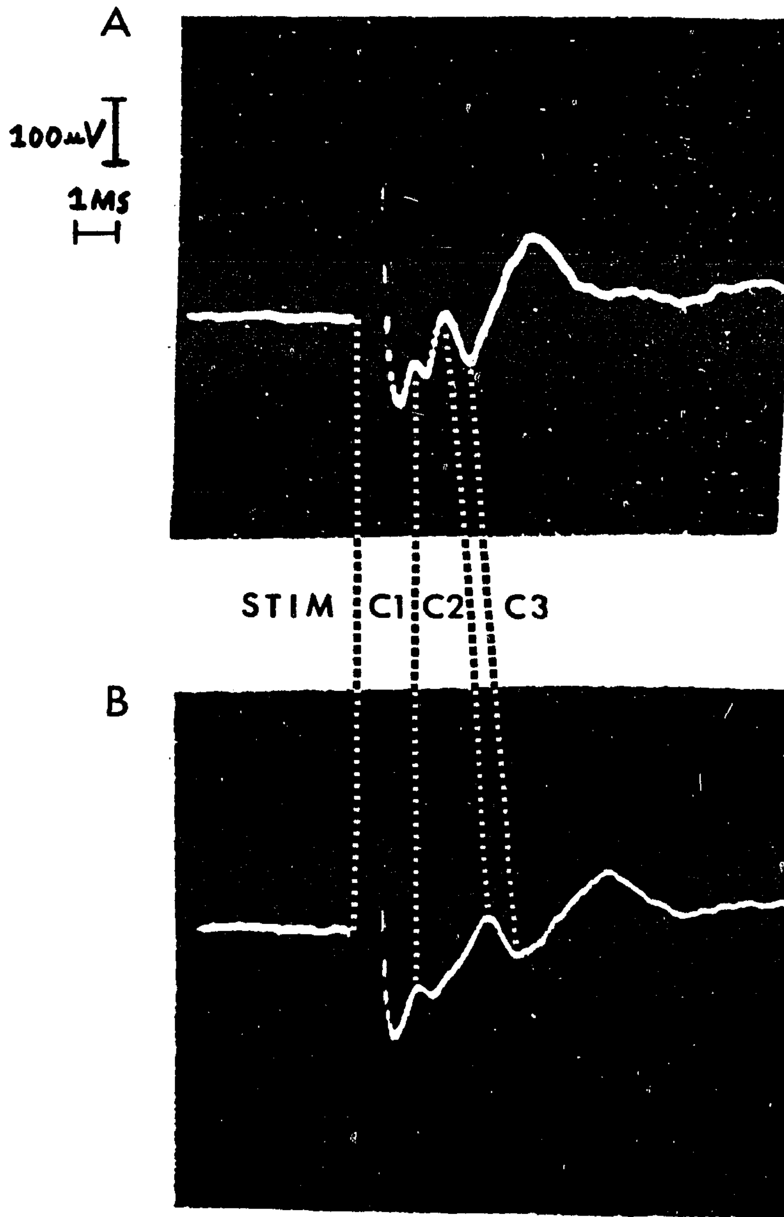


B
ptp RESPONSE AMPLITUDE (μV)
150
130
110
90
70
50
30
C3 MIN=5
C2 MIN=6
C1 MIN=6
THRESHOLD
0
100
200
300
400
500
STIMULUS ENERGY (nanoC)



C
100mV
1 MS
1
2
3
4
5
6
7

Figure 8. Demonstration of the fact that C2 and C3 of the response of the dorsal layers of the LGN to ON stimulation are time-locked. A. A response of the dorsal layers of the LGN to ON stimulation with short latency C2 and C3. B. A response of the dorsal layers of the LGN to ON stimulation with longer latency C2 and C3. Labelling as in Figure 5. The fact that the line connecting the two C1s is parallel to the "STIM" line indicates that the latency of C1 is the same in both A and B. The fact that the line connecting the two C2s and the line connecting the two C3s are not parallel to the "STIM" line (nor to the line connecting the two C1s) indicates that the two C2s have different latencies and that the two C3s have different latencies. The fact that the line connecting the two C2s is parallel to the line connecting the two C3s indicates that the difference in latency between C3 of A and C3 of B is exactly equal to the difference in latency between C2 of A and C2 of B. That is, C2 and C3 are time-locked. They vary in time together. Amplitude and time markers given next to A apply to B as well.


A
100uV
1MS
STIM
C1
C2
C3
B

2. Optic nerve response

The response of the ON to stimulation of the dorsal layers of the LGN usually consists of two components; rarely, a third component is seen. Several different responses were recorded, with no one response occurring predominantly. Figure 9 presents four such responses. All components have very low amplitudes (less than 100 uV), with later components tending to have higher amplitudes than earlier components. Latency of the first component has a range of .8-1.4 msec, with a median of 1.2 msec. The second component has a latency range of 1.5-2.4 msec. with a median of 1.9 msec.

B. Layer B of LGN

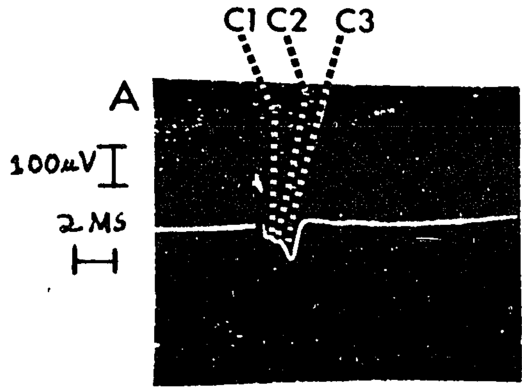
1. Response to ON stimulation

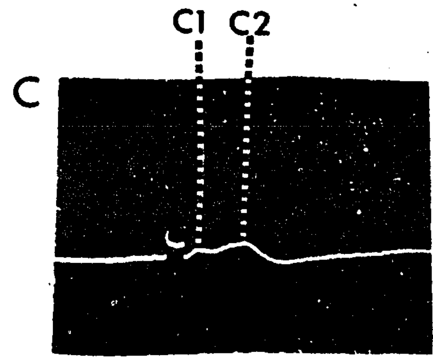
The response of layer B to ON stimulation consists of two components. Figure 10 presents latency, amplitude and threshold data for the response, and defines its two components. The median response latencies for the two components are 1.2 (range: 1.0-1.3) and 4.0 (range: 3.6-4.4) msec respectively. The median threshold energies for the two components are 35 and 100 nanoC respectively.

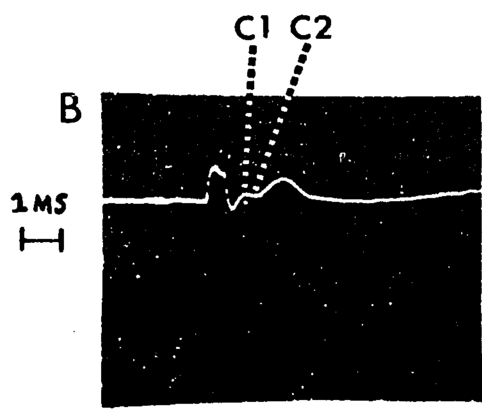
2. Optic nerve response

The response of the ON to stimulation of layer B usually consists of two components; rarely only one component is seen. Several different responses were recorded, with no one response occurring

Figure 9. Response of the ON to stimulation of layers A and A1 of the LGN. A, B, C and D depict four different responses, each from a different animal. Amplitude marker next to A applies to B, C and D as well. Time marker next to B applies to C and D as well.


C1 C2 C3
A
100µV
2 MS


C1 C2
C


C1 C2
B
1 MS

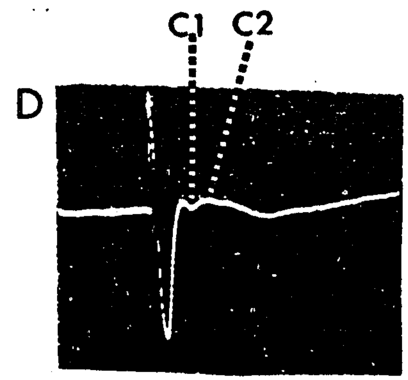
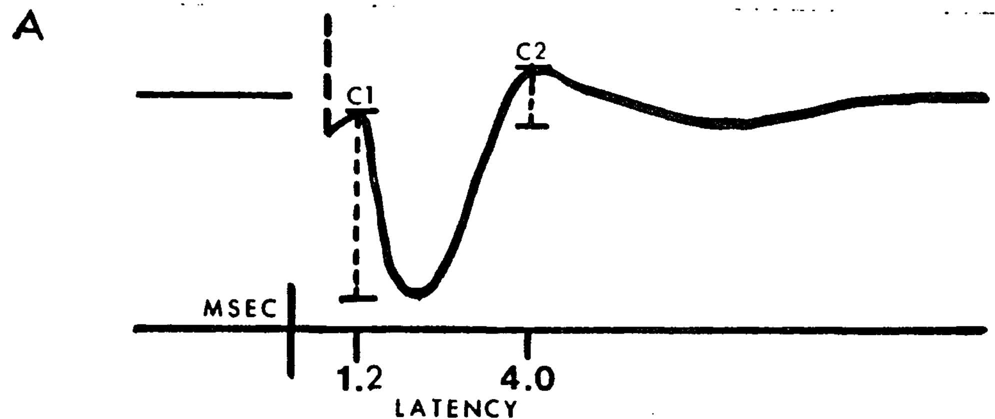
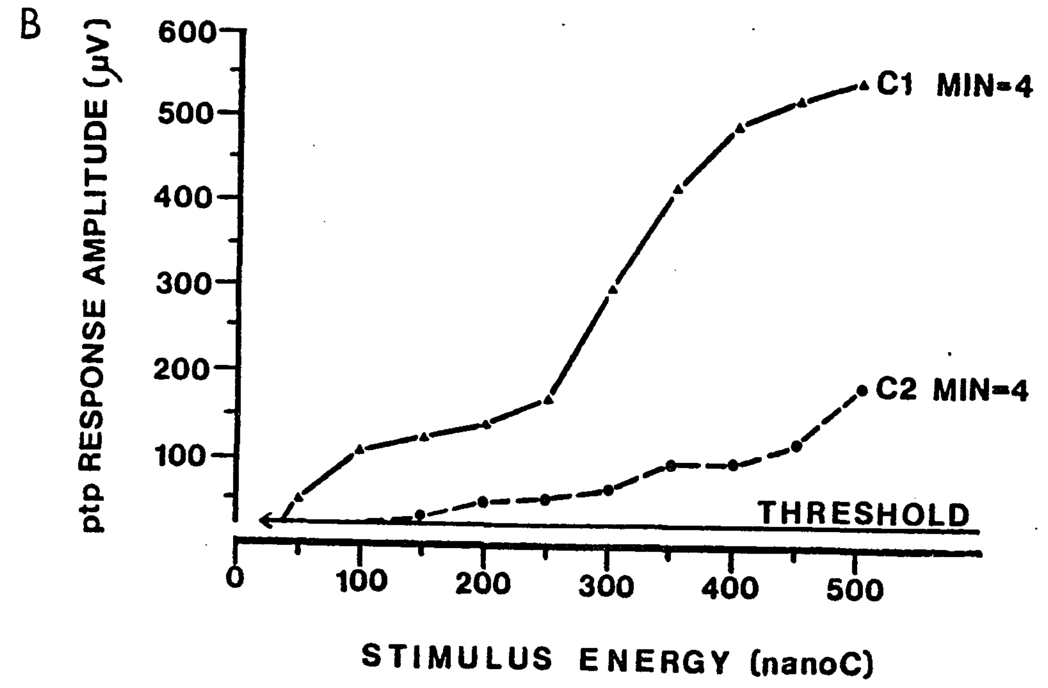
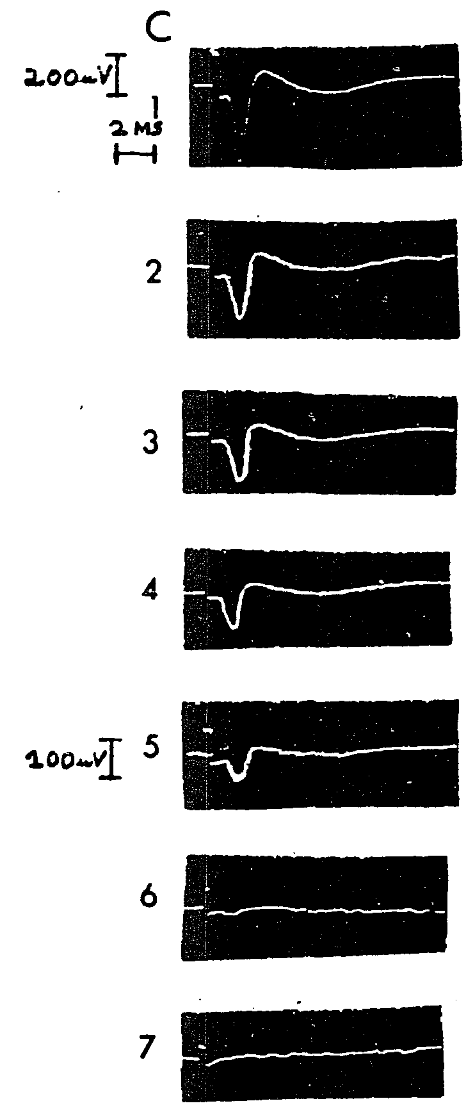

C1 C2
D

Figure 10. Response of layer B of the LGN to stimulation of the ON. A. A schematic drawing of the typical response. Labelling as in Figure 3A. B. Median peak to peak (ptp) amplitude of each of the two components of the response, presented as a function of stimulus energy. Labelling as in Figure 3B. C. Series of photographs of the response of layer B to decreasing stimulus energies applied to the ON. Time marker next to photo 1 applies to all other photos as well. Amplitude marker next to photo 1 applies to photos 2, 3 and 4 as well. Amplitude marker next to photo 5 applies to photos 6 and 7 as well. Photos 2, 3, 4 and 5 retouched.


A
C1
C2
MSEC
1.2
4.0
LATENCY


B
600
500
400
300
200
100
ptp RESPONSE AMPLITUDE (µV)
C1 MIN=4
C2 MIN=4
THRESHOLD
0
100
200
300
400
500
STIMULUS ENERGY (nanoC)


C
200µV
2 MS
2
3
4
5
100µV
6
7

predominantly. Figure 11 presents four such responses. All components have very low amplitudes (rarely more than 100 uV), with the first component tending to have a higher amplitude than the second component. Latency of the first component has a range of .9-1.3 msec, with a median of 1.1 msec. The second component has a latency range of 3.4-4.6 msec, with a median of 3.8 msec.

C. SC

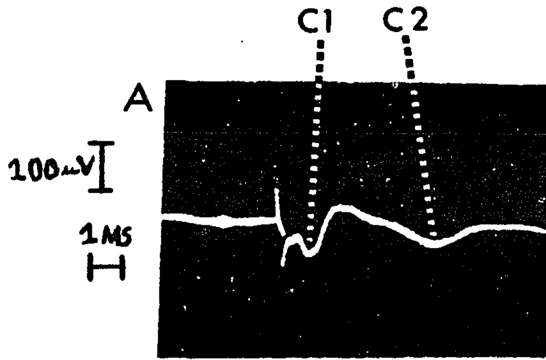
1. "Slow" response to ON stimulation

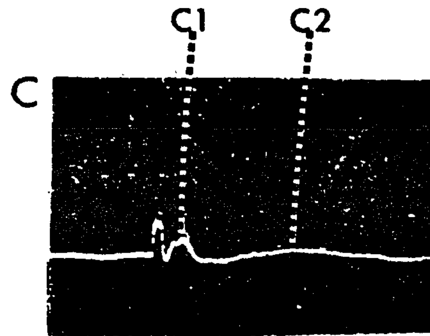
The "slow" response of the SC to ON stimulation consists of only one component. Figure 12 presents latency, amplitude and threshold data for the response, and defines its one component. The median response latency for this one component is 6.0 (range: 5.8-6.1) msec. The median threshold energy for this component is 20 nanoC.

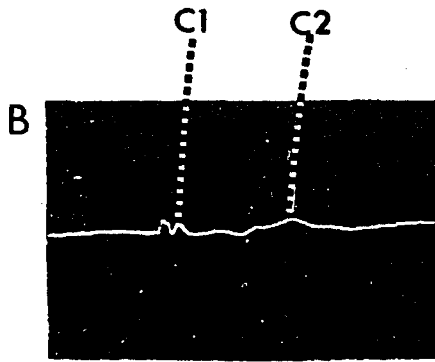
2. "Fast" response to ON stimulation

The "fast" response of the SC to stimulation of the ON consists of one, two or three components. Several different responses were recorded, with no one response occurring predominantly. Figure 13 presents four such responses. Early components (C1 and C2) have low amplitudes (less than 50 uV), while the later component (C3), when present, has a higher amplitude, sometimes reaching 200 uV. Latency of the first component has a range of 1.0-1.6 msec, with a median of 1.4 msec. The second component has a latency range of 1.4-2.5 msec, with a median of 2.0 msec. The third component has a

Figure 11. Response of the ON to stimulation of layer B of the LGN. A, B, C and D depict four different responses, each from a different animal. Amplitude and time markers next to A apply to B, C and D as well.


C1
C2
A
100µV
1MS


C1
C2
C


C1
C2
B

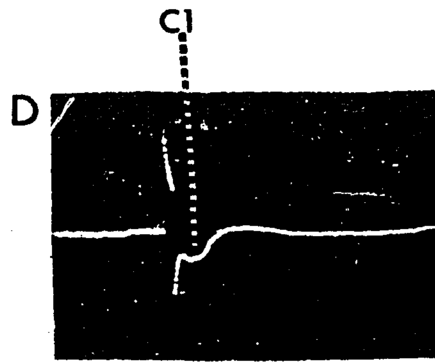
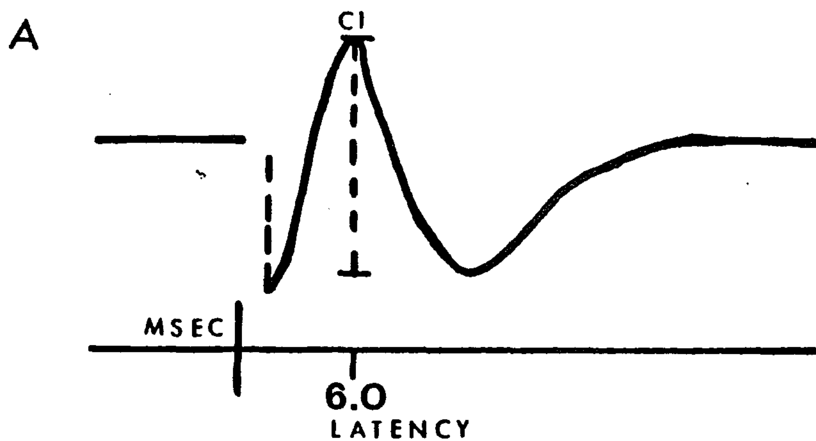
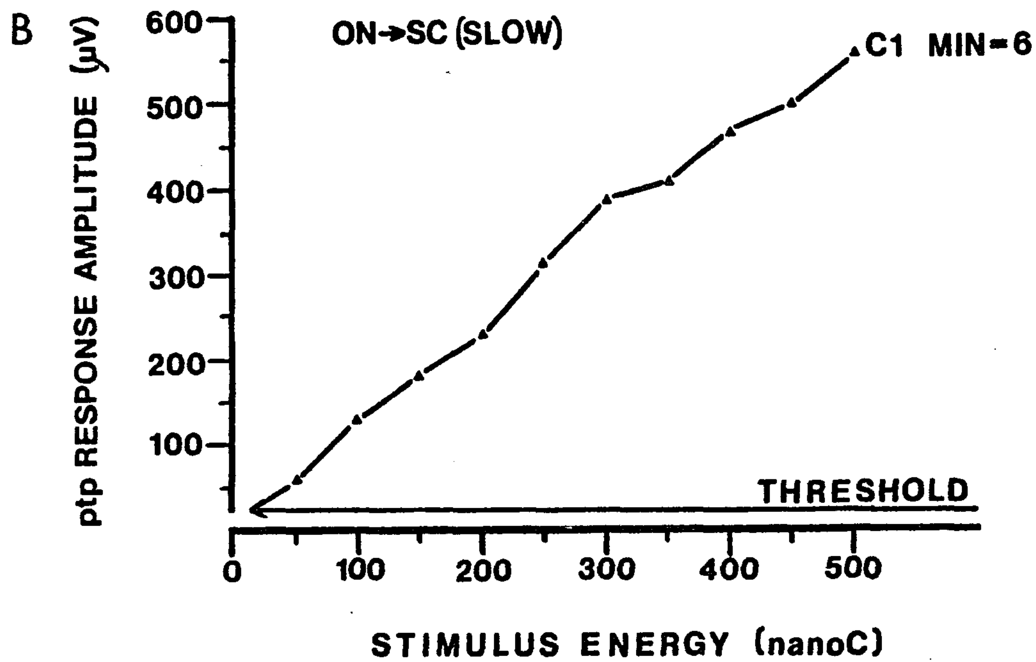

C1
D

Figure 12. "Slow" response of the SC to stimulation of the ON. A. A schematic drawing of the typical response. Labelling as in Figure 3A. B. Median peak to peak (ptp) amplitude of the one component of the response, presented as a function of stimulus energy. Labelling as in Figure 3B. C. Series of photographs of the "slow" response of the SC to decreasing stimulus energies applied to the ON. Time marker next to photo 1 applies to all other photos as well. Amplitude marker next to photo 1 applies to photos 2, 3, 4 and 5 as well. Amplitude marker next to photo 6 applies to photo 7 as well.


A
C1
MSEC
6.0
LATENCY


B
ON→SC (SLOW)
C1 MIN=6
ptp RESPONSE AMPLITUDE (µV)
600
500
400
300
200
100
THRESHOLD
0
100
200
300
400
500
STIMULUS ENERGY (nanoC)

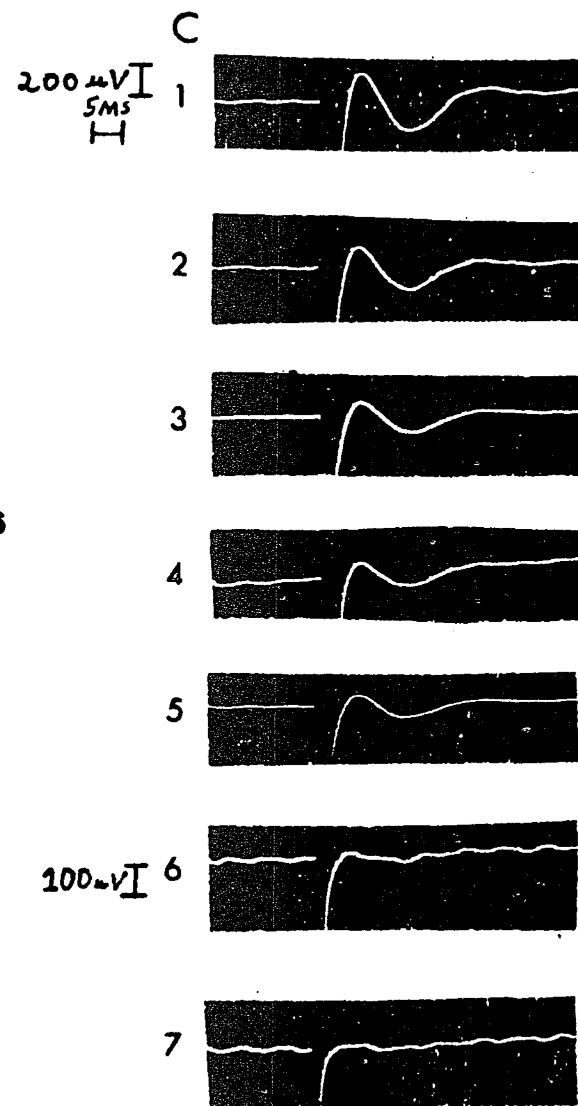
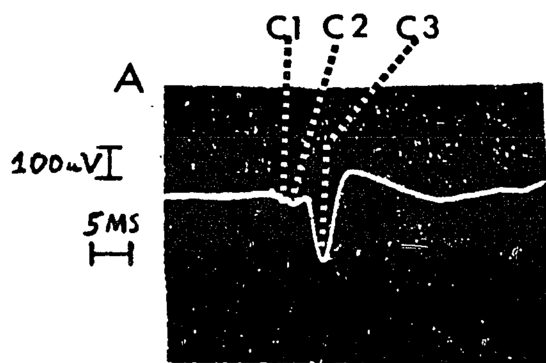

C
200 µV
5MS
1
2
3
4
5
100 µV
6
7

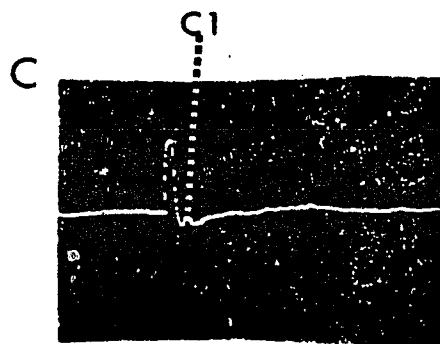
Figure 13. "Fast" response of the SC to stimulation of the ON. A, B, C and D depict four different responses, each from a different animal. Amplitude marker next to A applies to B, C and D as well. Time marker next to B applies to C and D as well.

ON → SC (FAST)

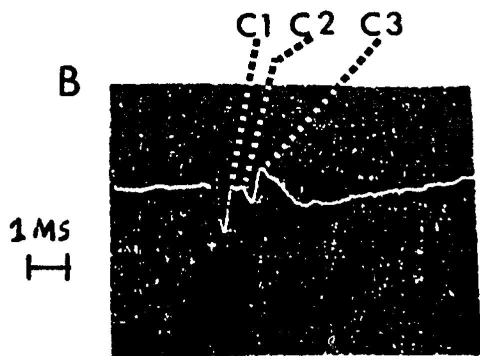
A



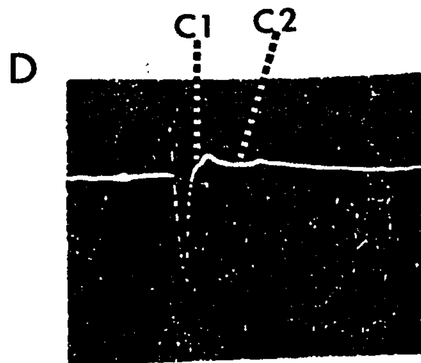
C



B



D



latency range of 1.9-5.8 msec, with a median of 3.2 msec.

3. Optic nerve response

The response of the ON to SC stimulation, at a given locus within the SC, is the same, whether ON stimulation elicits a "fast" or "slow" SC response from that locus. The response of the ON to SC stimulation consists of one component. Figure 14 presents latency, amplitude and threshold data for the response, and defines its one component. The median response latency for this component is 1.3 (range: 1.0-1.4) msec. The median threshold energy for this component is 350 nanoC.

D. PRT

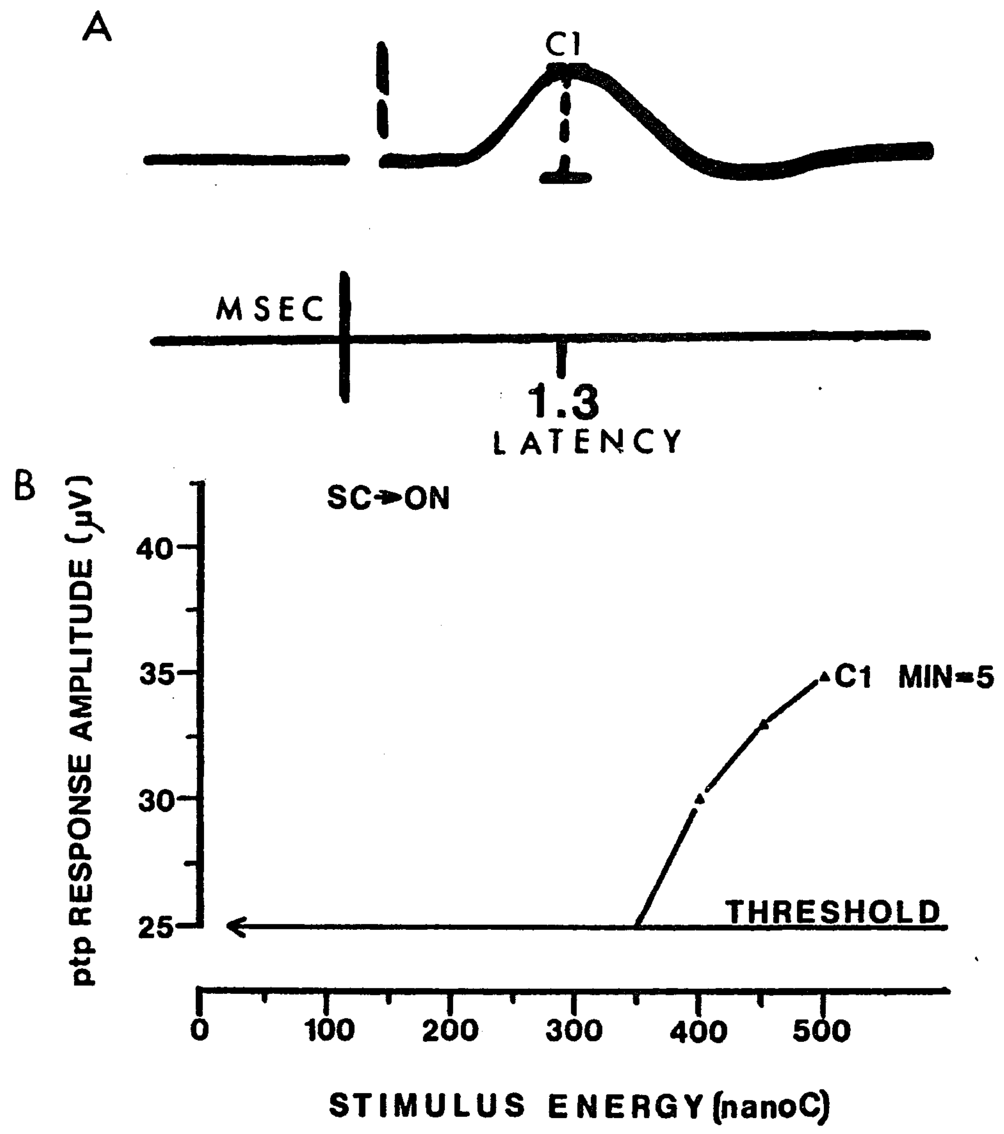
1. Response to ON stimulation

The response of the PRT to ON stimulation consists of only one component. Figure 15 presents latency, amplitude and threshold data for the response, and defines its one component. The median response latency for this one component is 6.4 (range: 6.2-6.5) msec. The median threshold energy for this component is 25 nanoC.

2. Optic nerve response

The response of the ON to PRT stimulation usually consists of two components, occasionally only one component is seen. Several different responses were recorded, with no one response occurring

Figure 14. Response of the ON to stimulation of the SC. A. A schematic drawing of the typical response. Labelling as in Figure 3A. B. Median peak to peak (ptp) amplitude of the one component of the response, presented as a function of stimulus energy. Labelling as in Figure 3B. C. Series of photographs of the response of the ON to decreasing stimulus energies applied to the SC. Time and amplitude markers next to photo 1 apply to all other photos as well.


A
C1
MSEC
1.3
LATENCY
B
SC→ON
ptp RESPONSE AMPLITUDE (μV)
40
35
30
25
C1 MIN=5
THRESHOLD
0
100
200
300
400
500
STIMULUS ENERGY (nanoC)

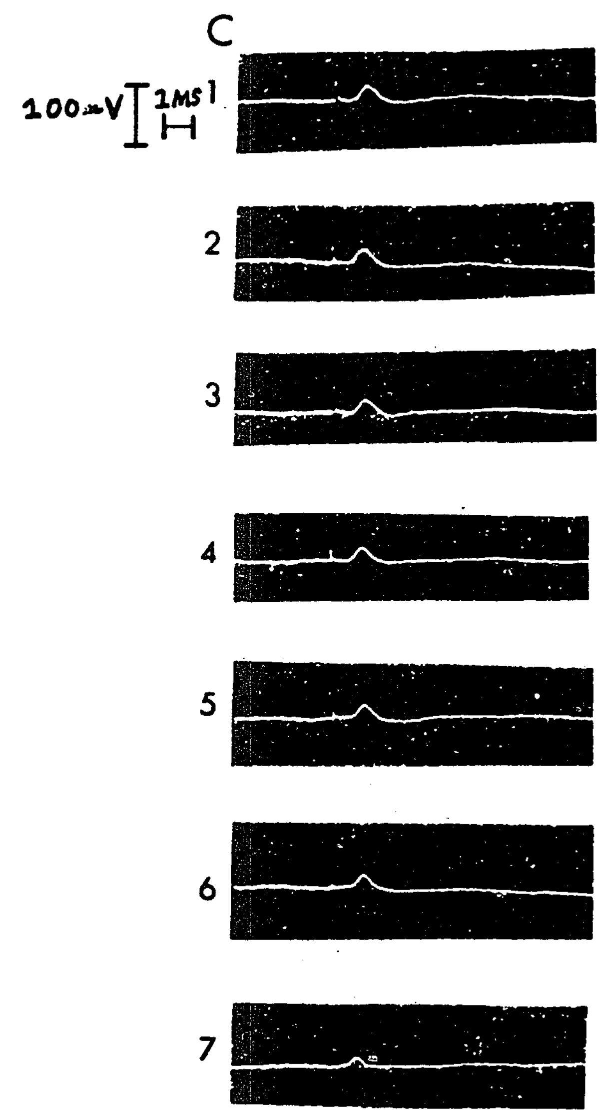
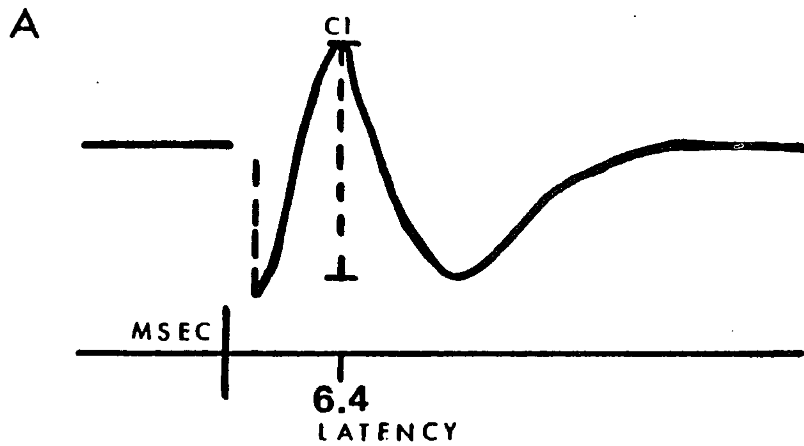
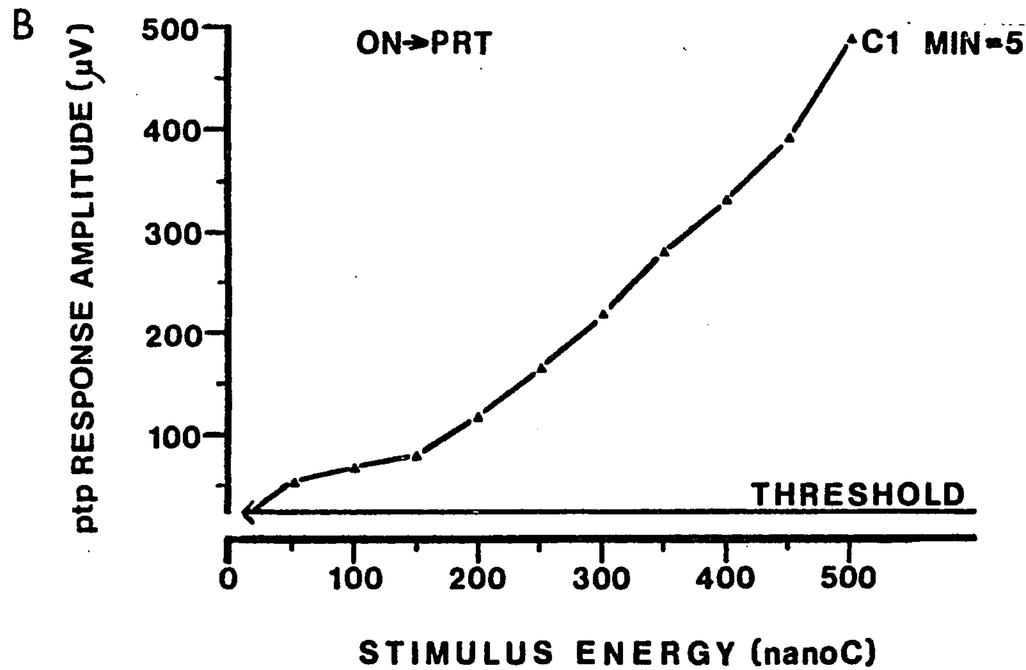
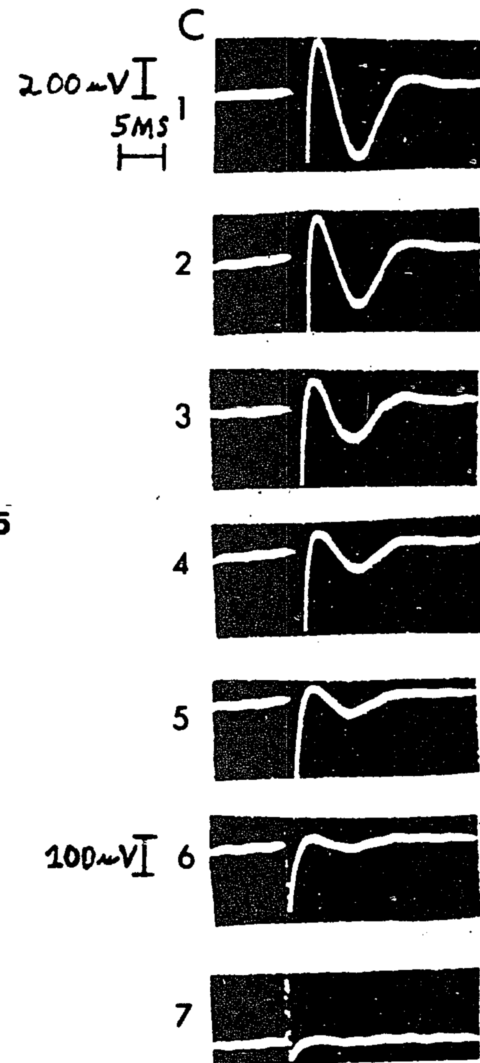

C
100μV
1MS
1
2
3
4
5
6
7

Figure 15. Response of the PRT to stimulation of the ON. A. A schematic drawing of the typical response. Labelling as in Figure 3A. B. Median peak to peak (ptp) amplitude of the one component of the response, presented as a function of stimulus energy. Labelling as in Figure 3B. C. Series of photographs of the response of the PRT to decreasing stimulus energies applied to the ON. Time marker next to photo 1 applies to all other photos as well. Amplitude marker next to photo 1 applies to photos 2, 3, 4 and 5 as well. Amplitude marker next to photo 6 applies to photo 7 as well.


A
C1
MSEC
6.4
LATENCY


B
500
400
300
200
100
ptp RESPONSE AMPLITUDE (μV)
ON→PRT
C1 MIN=5
THRESHOLD
0
100
200
300
400
500
STIMULUS ENERGY (nanoC)


C
200 μV
5MS
1
2
3
4
5
100 μV
6
7

predominantly. Figure 16 presents four such responses. Both components have very low amplitudes (rarely reaching 50 uV). Latency of the first component has a range of 1.0-1.6 msec, with a median of 1.2 msec. The second component has a latency range of 1.5-2.4 msec, with a median of 1.8 msec.

F. PUL

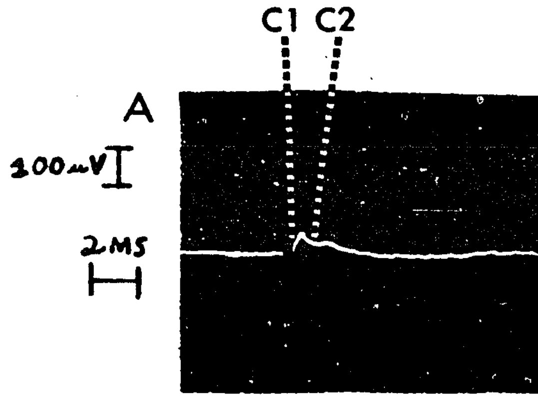
The response of the PUL to ON stimulation usually consists of three components; occasionally only two components are seen. Several different responses were recorded, with no one response occurring predominantly. Figure 17 presents four such responses. The earlier components (C1 and C2) have lower amplitudes, rarely reaching 100 uV (usually less than 50 uV). The last component (C3) has a larger amplitude, but it rarely reaches 200 uV, and is usually less than 100 uV. Latency of the first component has a range of 1.3-1.8 msec, with a median of 1.5 msec. The second component has a latency range of 1.9-3.0 msec, with a median of 2.4 msec. The third component has a latency range of 2.8-4.8 msec, with a median of 3.5 msec. There was no response of the ON upon stimulation of the PUL.

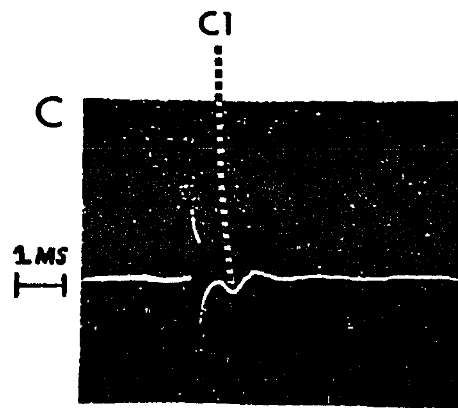
G. MRF

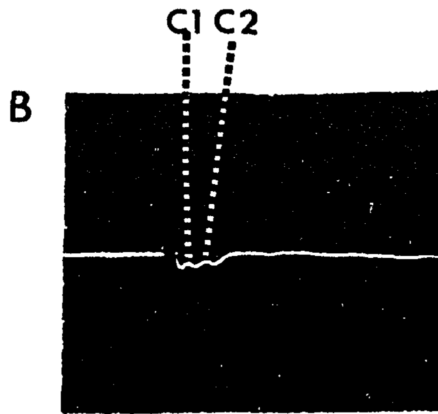
The MRF produced no response upon stimulation of the ON, and there was no ON response upon stimulation of the MRF.

Figure 16. Response of the ON to stimulation of the PRT. A, B, C and D depict four different responses, each from a different animal. Amplitude and time markers next to A apply to B, C and D as well.

PRT → ON







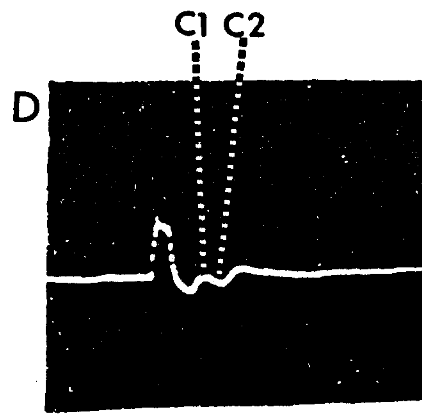
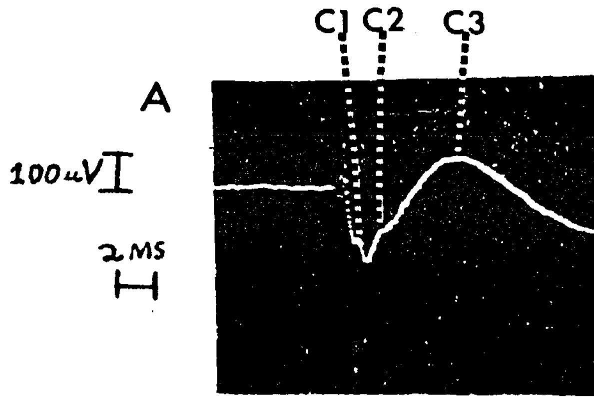


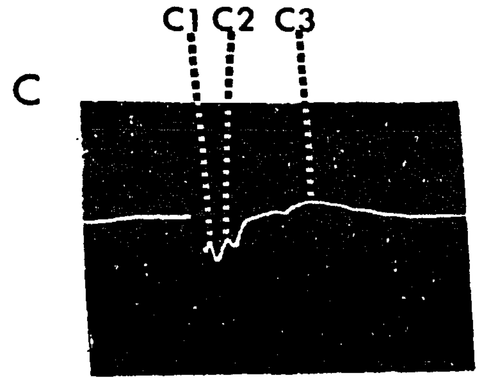
Figure 17. Response of the PUL to stimulation of the ON. A, B, C and D depict four different responses, each from a different animal. Amplitude and time markers next to A apply to B, C and D as well.

ON → PUL

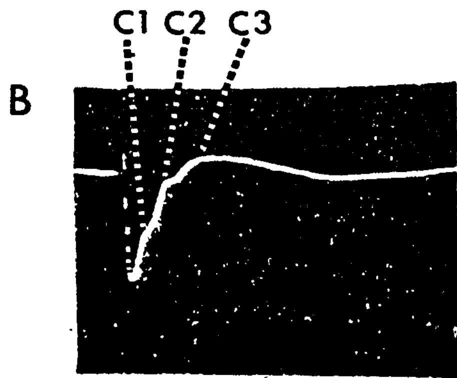
A



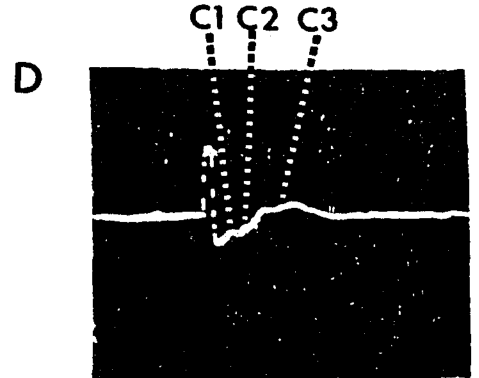
C



B



D



H. 2 mm below SC

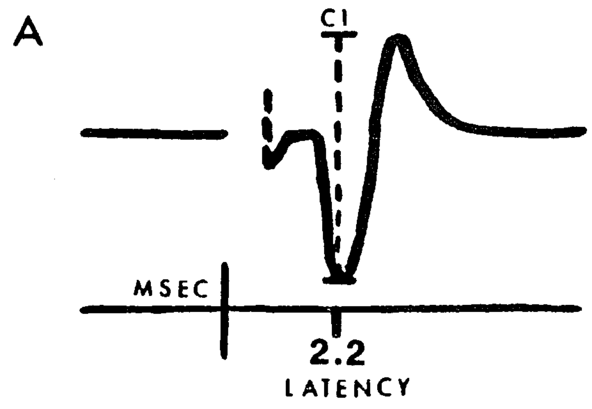
Upon stimulation of an area approximately 2 mm below the SC and just lateral to the central gray, a large amplitude response was recorded from the ON. This response consists of one component. Figure 18 presents latency, amplitude and threshold data for the response, and defines its one component. The median latency of the one component is 2.2 (range: 2.0-2.5) msec. No response was recorded from this area upon stimulation of the ON.

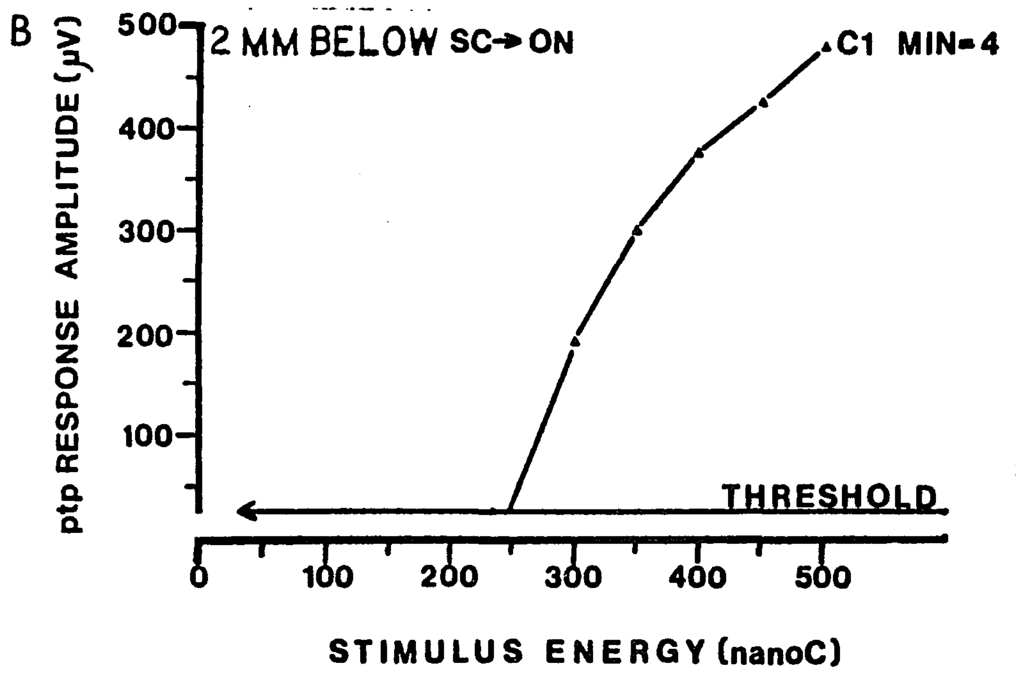
IV. LAON afferents and efferents

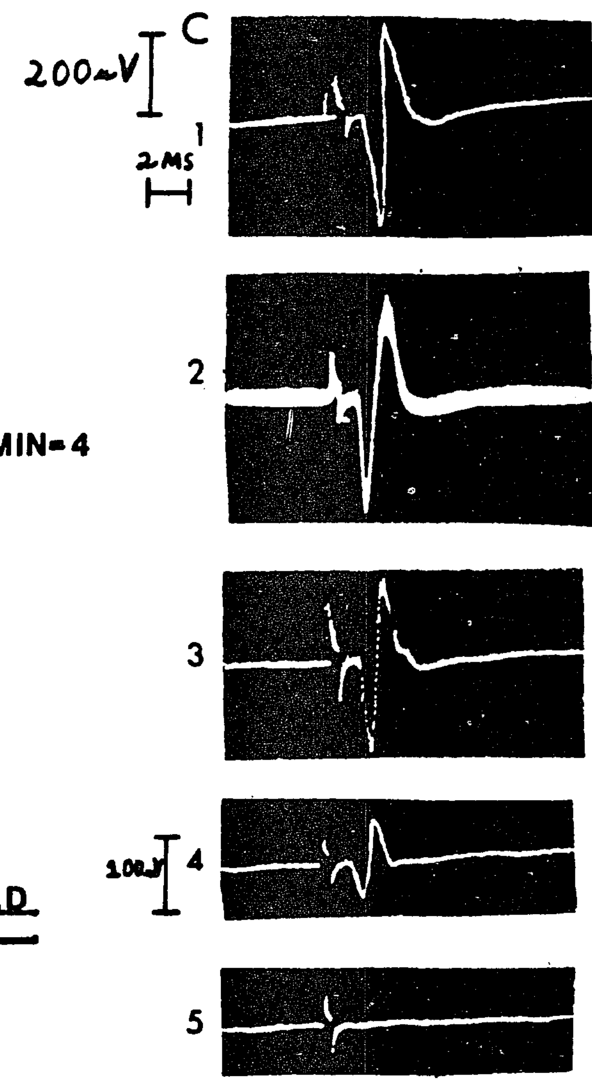
The responses of all three layers of the LGN to stimulation of the LAON are the same, as are the responses of the LAON upon stimulation of all three layers of the LGN. So, the dorsal and ventral layers of the LGN will be collectively referred to as just the LGN in this section. Also, the response of the SC upon LAON stimulation, and that of the LAON upon SC stimulation, is the same, whether a "slow" or "fast" SC response is elicited upon ON stimulation in any given cat.

The responses of the LGN, SC, PRT, PUL and MRF upon stimulation of the LAON and those of the LAON upon stimulation of the LGN, SC, PRT, PUL and MRF are very similar in waveform, latency and other characteristics. In particular, the responses of the LGN, SC, PRT, PUL and MRF to LAON stimulation, and those of the LAON to stimulation of these five structures, typically consist of two components. The first component has a short latency and smaller amplitude.

Figure 18. Response of the ON to stimulation of an area about 2 mm below the SC. A. A schematic drawing of the typical response. Labelling as in Figure 3A. B. Median peak to peak (ptp) amplitude of the one component of the response, presented as a function of stimulus energy. Labelling as in Figure 3B. C. Series of photographs of the response of the ON to decreasing stimulus energies applied to the area about 2 mm below the SC. Photo 2 is the same as photo 1 but it depicts five superimposed sweeps. Time marker next to photo 1 applies to all other photos as well. Amplitude marker next to photo 1 applies to photos 2 and 3 as well. Amplitude marker next to photo 4 applies to photo 5 as well. Photos 1 and 4 retouched. Note the similarity in waveform, latency and amplitude of this response to those of C2 of the ON response to LAON stimulation seen in Figure 6A, B and C.


A
C1
MSEC
2.2
LATENCY


B
2 MM BELOW SC→ON
C1 MIN=4
THRESHOLD
ptp RESPONSE AMPLITUDE (µV)
500
400
300
200
100
0
100
200
300
400
500
STIMULUS ENERGY (nanoC)


C
200µV
2MS
1
2
3
4
5

The second component has a long latency and large amplitude. The range of median latencies of the C1s of the LAON responses to stimulation of the LGN, SC, PRT, PUL and MRF is .9-1.4 msec. The range of median latencies of the C2s of these responses is 6.1-6.4 msec. The range of median latencies of the C1s of the responses of the LGN, SC, PRT, PUL and MRF to stimulation of the LAON is .9-1.5 msec. The range of median latencies of the C2s of these responses is 6.0-6.3 msec. The exact values of the latency of each component of each of these responses are presented in Table IV.

Since many characteristics, such as number of components, latency of components and threshold of components are very similar among these ten responses, only one of them will be illustrated. Figure 19 presents latency, amplitude and threshold data for the response of the LGN to stimulation of the LAON, and defines its two components.

The first component of all these responses was not always present, and even when present, was not always well defined. As can be seen from Figure 19B, the amplitude of the C2s of these responses is much larger, perhaps by a factor of 10, than responses elicited by stimulation of, or recorded from, the ON.

The response of the area about 2 mm below the SC to stimulation of the LAON differs from those of the LGN, SC, PRT, PUL and MRF. The response of this area to LAON stimulation typically consists of two small, short latency components. Several different responses were recorded, with no one response occurring predominantly. Figure 20 presents two such responses. Both components have very low amplitudes, rarely reaching 50 uV. Latency of the first component has a range of .5-.7 msec; that of the second component

Table IV. Meidan latency (in msec) of the two components of the responses of the LGN, SC, PRT, PUL and MRF to LAON stimulation, and of those of the responses of the LAON to stimulation of the LGN, SC, PRT, PUL and MRF. The arrow indicates the direction of stimulation-recording.

	C1	C2
Responses	Latency	Latency
LAON LGN	.9	6.3
LAON SC	1.5	6.0
LAON PRT	1.3	6.3
LAON PUL	1.3	6.0
LAON MRF	.9	6.3
LGN LAON	1.2	6.2
SC LAON	1.0	6.4
PRT LAON	1.4	6.4
PUL LAON	.9	6.1
MRF LAON	1.0	6.4

Figure 19. Response of the LGN to stimulation of the LAON. A. A schematic drawing of the typical response. Labelling as in Figure 3A. B. Median peak to peak (ptp) amplitude of each of the two components, presented as a function of stimulus energy. Labelling as in Figure 3B. C. Series of photographs of the response of the LGN to decreasing stimulus energies applied to the LAON. Time marker next to photo 1 applies to all other photos as well. Amplitude marker next to photo 1 applies to photo 2 as well; that next to photo 3 applies to photo 4 as well, and that next to photo 5 applies to photo 6 as well.

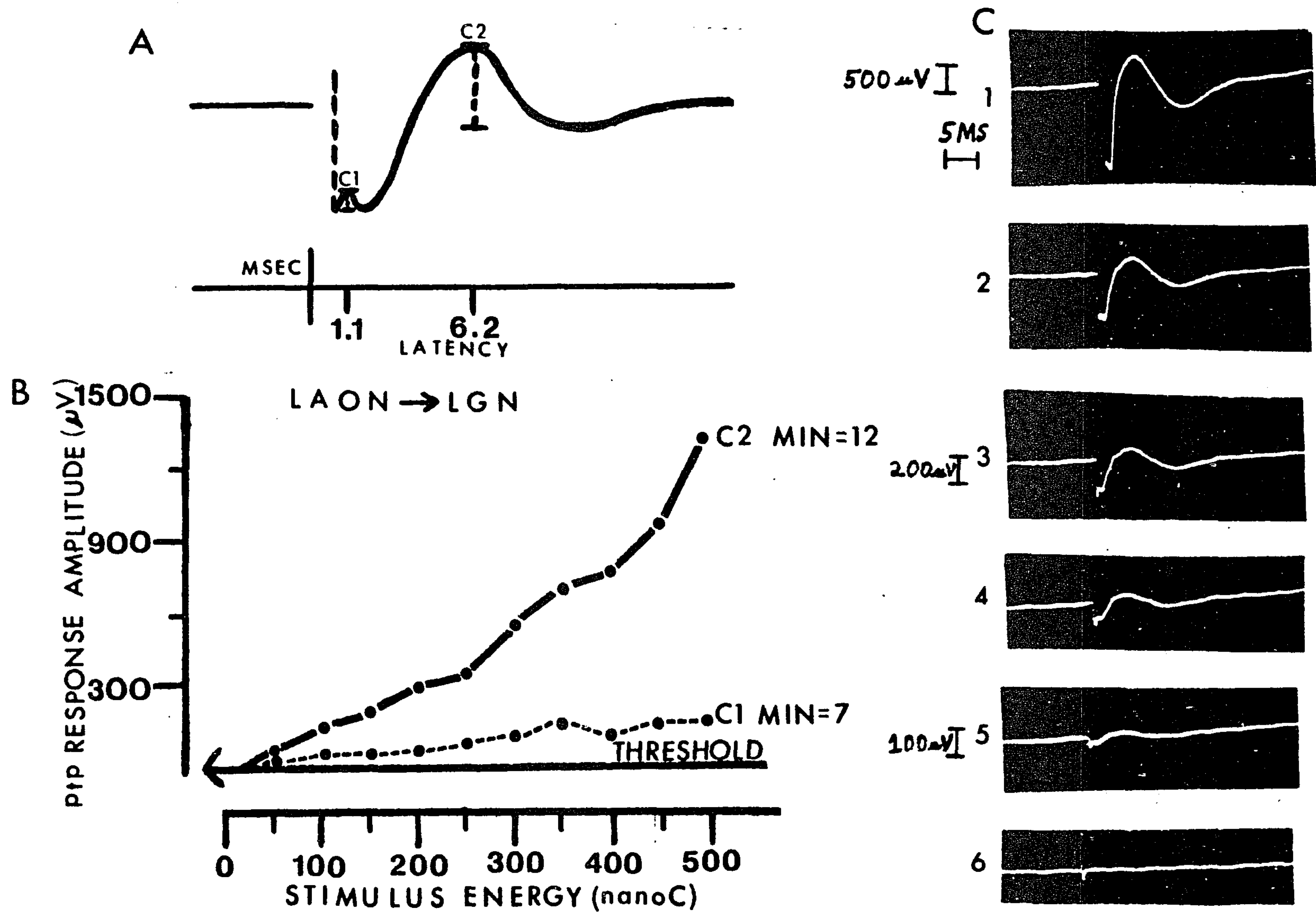
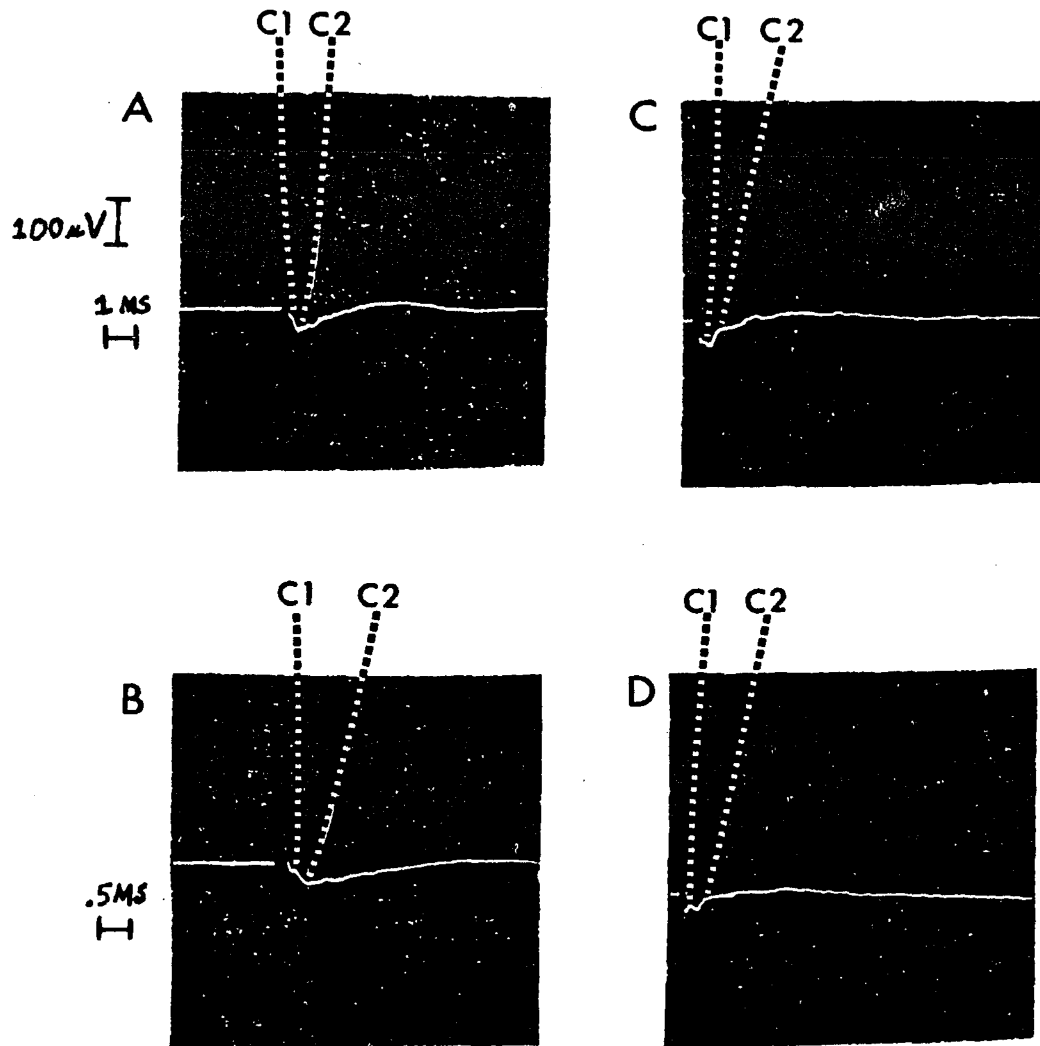

A
C2
C1
MSEC
1.1
6.2
LATENCY
B
1500
900
300
PtP RESPONSE AMPLITUDE (μV)
LAON → LGN
C2 MIN=12
C1 MIN=7
THRESHOLD
0
100
200
300
400
500
STIMULUS ENERGY (nanoC)
C
500 μV
5MS
1
2
200 μV
3
4
100 μV
5
6

Figure 20. Response of the area about 2 mm below the SC to stimulation of the LAON. A and B depict the same response, but with different time bases. C and D depict a different response from that depicted in A and B. The response depicted in A and B comes from a different animal from that depicted in C and D. Note the variability in degree of clarity of definition of the two components of the response depicted in C and D. That is, C1 is more prominent, more clearly seen in D than in C, while the reverse is true of C2. Amplitude marker next to A applies to B, C and D as well. Time marker next to B applies to C and D as well.


LAON → 2 MM BELOW SC
A
B
C
D
C1 C2
C1 C2
C1 C2
C1 C2
100μV
1 MS
.5MS

is .8-1.1 msec. This response is a rather tenuous one. The components tend to be rather unstable, as can be seen from a comparison of Figure 20C with 20D.

IV Histology

A. LAON

The full extent of the LAON is rarely shown in cat brain atlases, and is labelled even less often. Therefore, in order to depict the loci in and around the LAON from which data were obtained in the present study, it was necessary to select a series of sections that shows the LAON in its various positions along the lateral surface of the midbrain, and to enlarge the area around the LAON of each of these sections, so as to be able to plot the loci of electrode tips in the area. This was done in Figures 21 and 22. As can be seen in Figure 22, the electrode tip actually penetrated the nucleus, or reached its border, in ten cats. But, data were rarely obtained from a locus more than 1 mm away from the nucleus. Figures 23 and 24 show a typical penetration of the LAON by the electrode tip.

B. SC, MRF, 2 mm below SC

Figure 25 presents plates from the cat brain atlases of Jasper and Ajmone-Marsan (1954) and Fifkova and Marsal (1967), upon which are plotted the loci from which data were obtained from the SC, MRF and the area about 2 mm below the SC. As can be seen in the plate

Figure 21. Selected photographs of coronal sections of cat brain. From photo 1 to photo 10, the sections go in an approximate antero-posterior direction, from about A 5.0 to A 2.5. Marked off by a white box in each photo is the area containing the LAON which is further enlarged in Figure 22. In each photo, the arrow points to the LAON. Notice how the LAON changes in position ventrodorsally along the lateral wall of the midbrain as the sections proceed in an anteroposterior direction. Magnification: about X 5.

L A O N

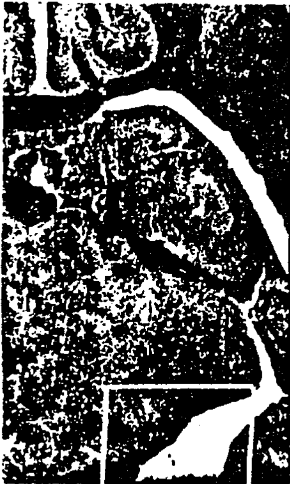
1

2

3

4

5


6

7

8

9

10

Figure 22. Series of enlargements of the areas marked off by white boxes in the photos in Figure 21. Numbers of photos in Figure 22 correspond to those in Figure 21. The LAON is outlined in white in each photo. Loci from which all LAON data were obtained are indicated by black squares (on light background) and white squares (on dark background). Magnification: about X 3.

LAON

1

6

2

7

3

8

4

9

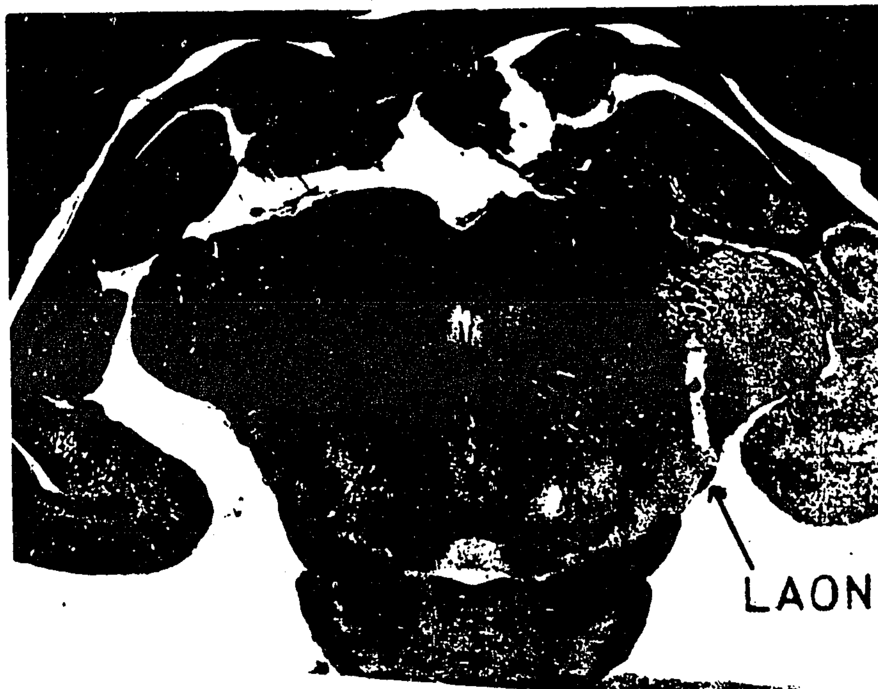
5

10

Figure 23. Two serial sections of cat brain showing the path of the electrode into (and/or burn mark in) the LAON. In A is shown the electrode tip approaching the dorsal aspect of the LAON. In B (about A 3.5), the electrode tip has entered the dorsal part of the LAON and the burn has destroyed it. Note the slight difference in color (more clearly seen in Figure 24B) between the dorsal and ventral parts of the nucleus, caused by the burn. Magnification: about X 4.

LAON

A



B

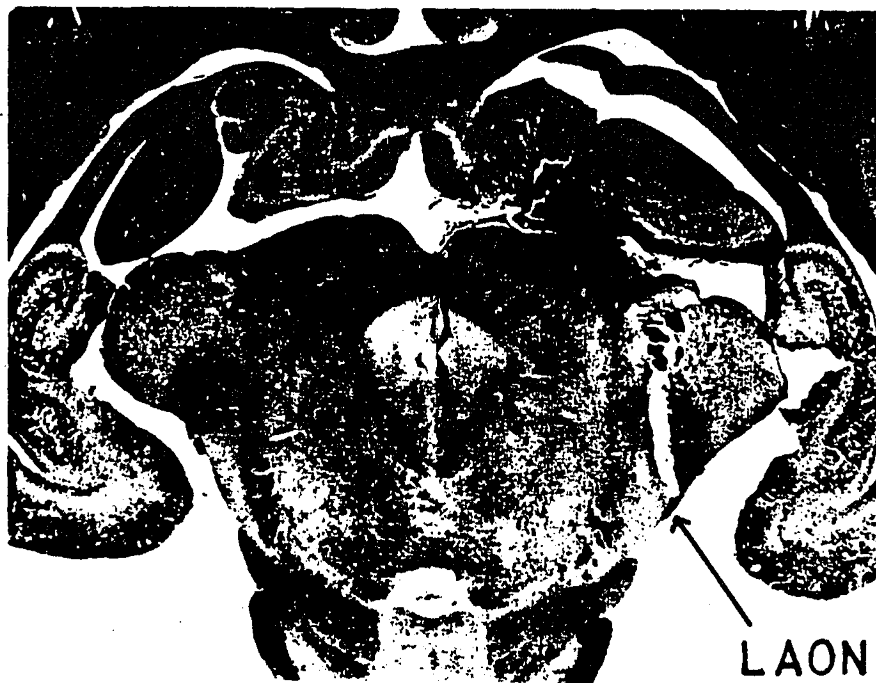
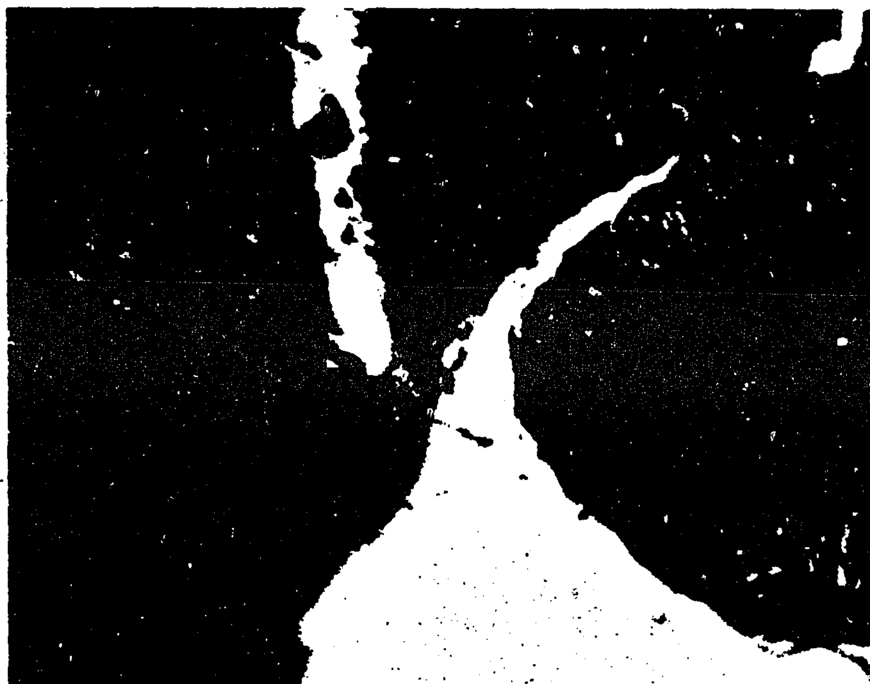


Figure 24. Enlargement of area around LAON in Figure 23. A. and B. Enlargements of area around LAON in Figures 23A and B respectively. Magnification: about X 10.

LAON

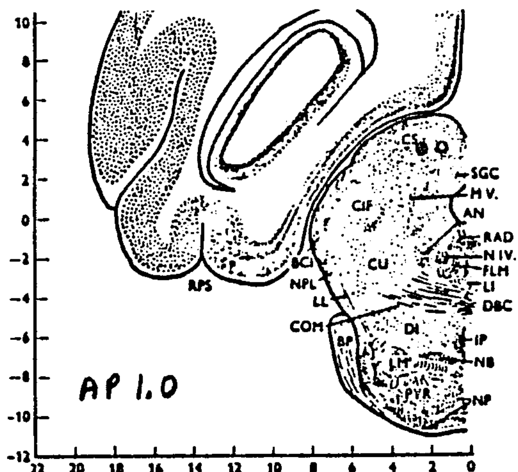
A

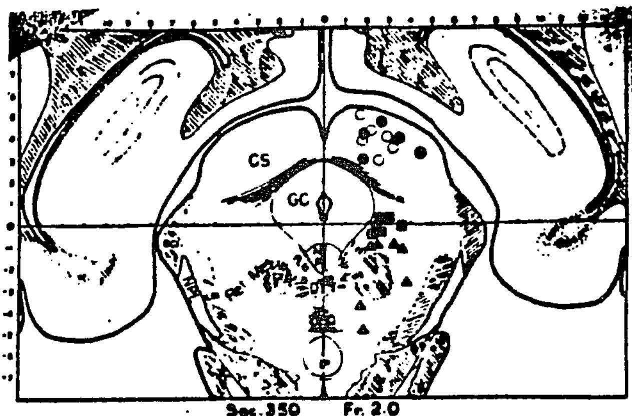


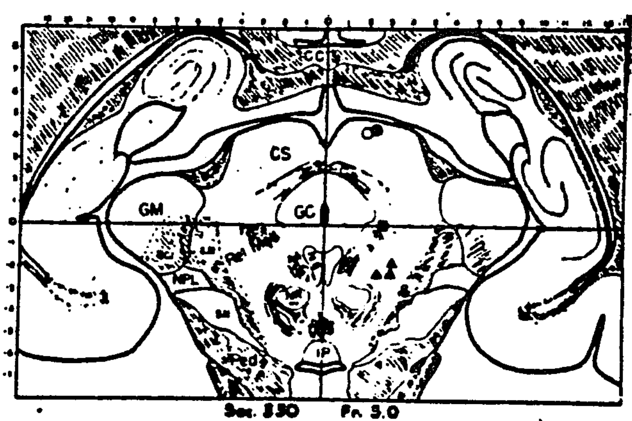
B

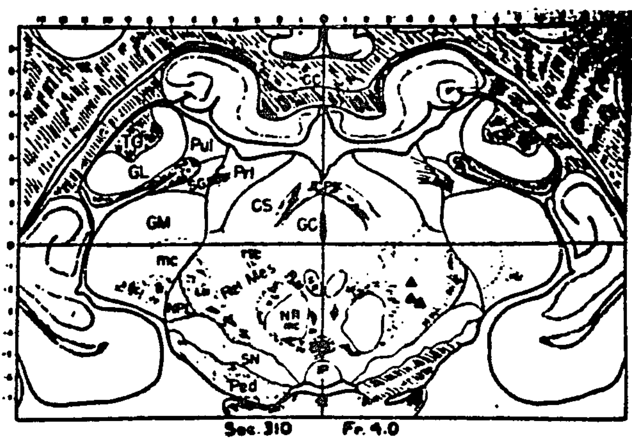
Figure 25. Series of schematic coronal sections upon which are plotted the loci within the SC, MRF and the area about 2 mm below the SC from which data were obtained. Plates labelled Fr. 2.0, Fr. 3.0 and Fr. 4.0 are from Jasper and Ajmone-Marsan (1954). That labelled AP 1.0 is from Fifkova and Marsala (1967). (This level [AP 1.0] is not shown in the atlas of Jasper and Ajmone-Marsan [1954]). All electrode loci were on the right side of the brain in the present study; however, only the left side of the brain is depicted in Fifkova and Marsala (1967). Open circles represent loci from which the "fast" SC response was recorded. Closed circles represent loci from which the "slow" SC response was recorded. Triangles represent loci within the MRF and squares represent loci wothin the area about 2 mm below the SC.

SC, MRF, 2MM BELOW SC









labelled Fr 2.0 in Figure 25, the squares are just above the triangles in many cases. Yet, responses were recorded from the ON upon stimulation at the loci represented by the squares, but not from the loci represented by the triangles (MRF). In addition, it can also be seen in Figure 25 that there is no apparent pattern to the location of sites from which the "slow" and "fast" SC responses were recorded. The loci from which both of these SC responses were recorded are strewn throughout much of the nucleus.

In Figure 26A is presented a typical locus, within the SC, from which data were obtained. In Figure 26B are presented loci from which data were obtained in the area about 2 mm below the SC and in the MRF.

C. PRT

In Figure 27, it can be seen that a number of loci from which PRT data came are on the border of the PRT with other structures (usually the SC). Yet, the response elicited from the loci plotted in Figure 27 all had similar response characteristics (such as number of components and latency and amplitude of components). Figure 28B presents a photograph of an actual histological section, with a burn mark in the dorsalmost aspect of the PRT.

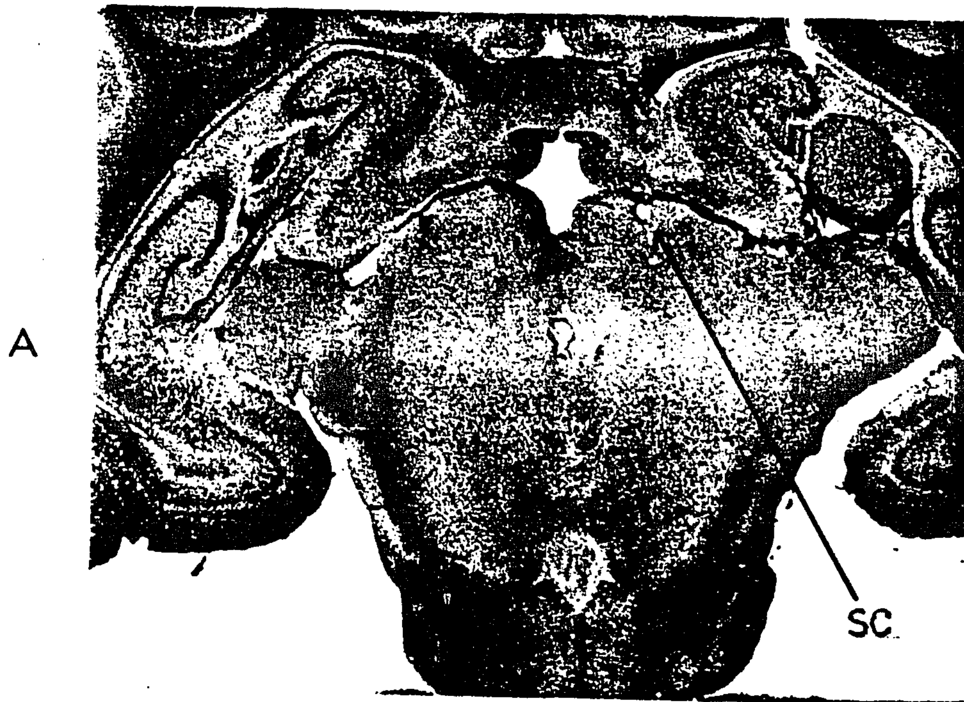
D. LGN and PUL

Figure 28A shows typical electrode penetrations into the dorsal and ventral layers of the LGN and the PUL. While the burn marks in

Figure 26. Coronal sections of cat brain showing representative electrode penetrations in the SC, MRF and the area about 2 mm below the SC. A. Sections at about A 2.5. Small burn mark is seen in the dorsal aspect of the SC. B. Section at about A 2.0. The dorsal-most burn mark is in the area about 2 mm below the SC. The ventral-most burn mark is in the MRF. Magnification: about X 4.

SC, MRF, 2 MM BELOW SC

A



B

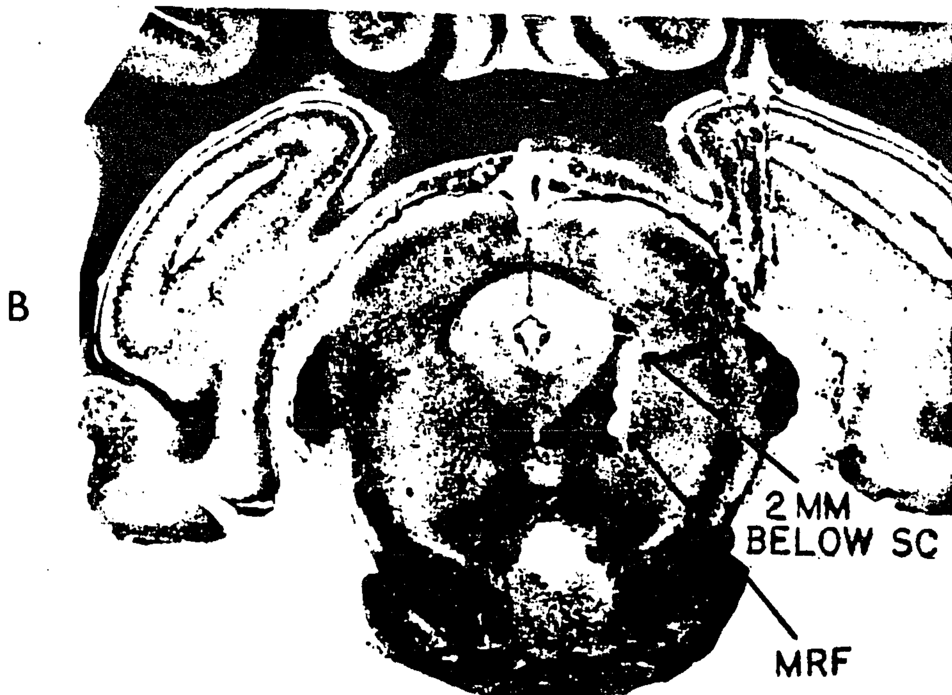
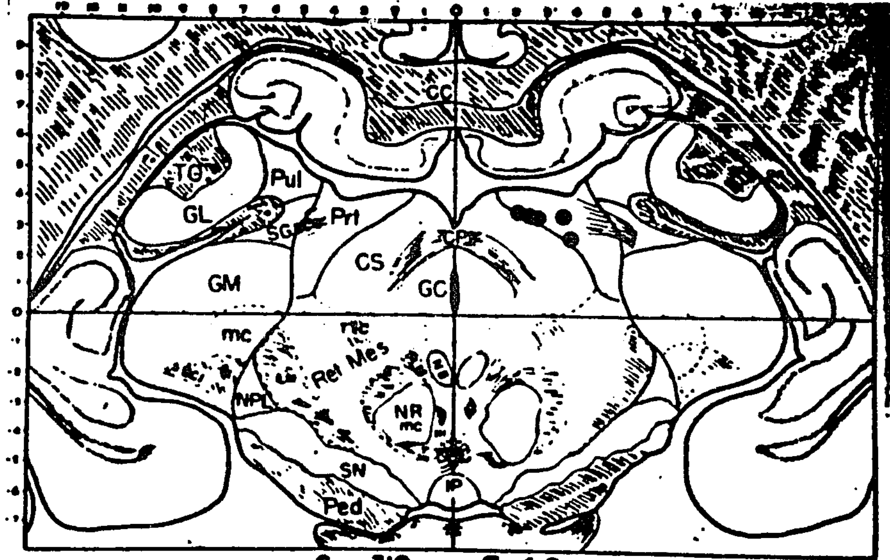


Figure 27. Schematic coronal sections, from the cat brain atlas of Jasper and Ajmone-Marsan (1954), upon which are plotted the loci within the PRT from which responses were recorded upon stimulation of the ON.

PRETECTUM



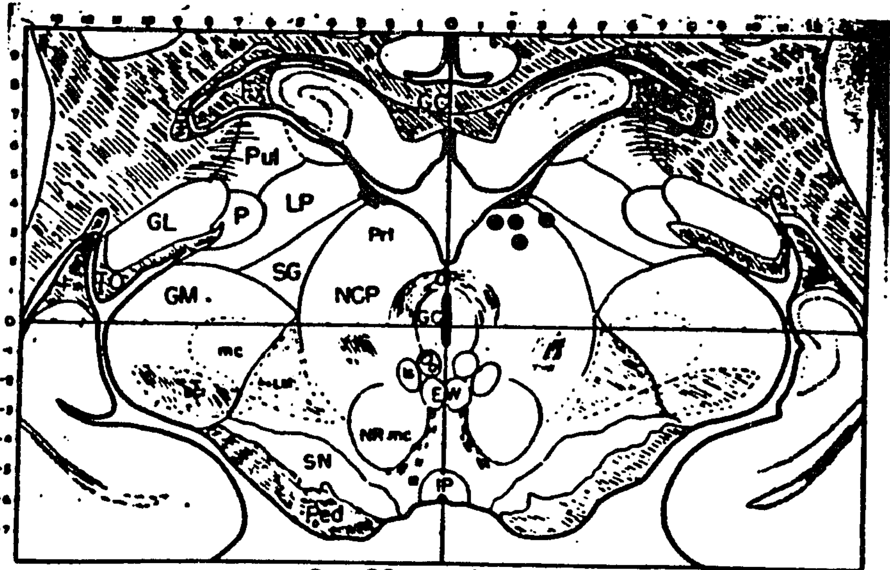
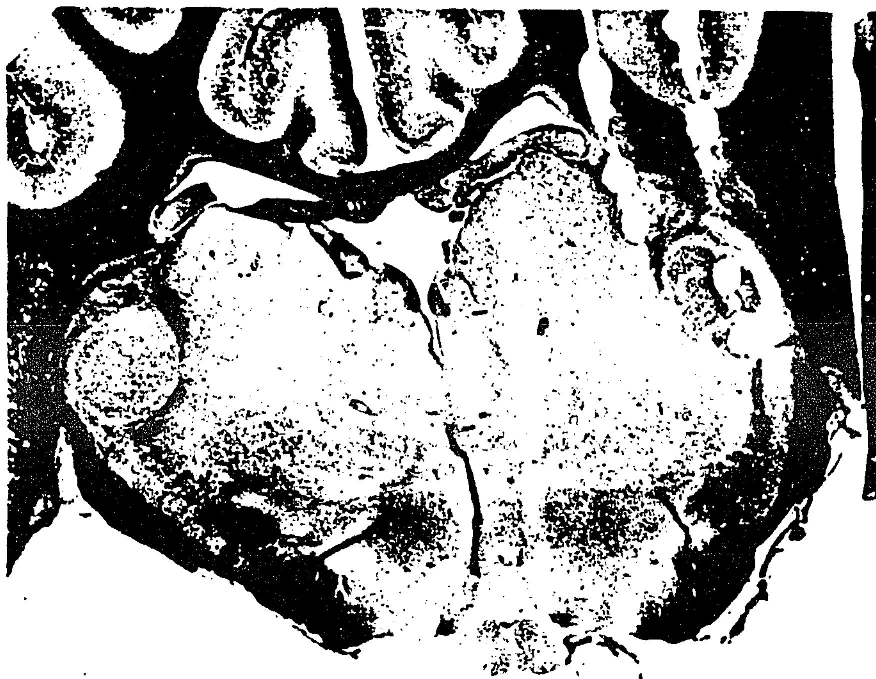


Figure 28. Coronal sections of cat brain showing representative electrode penetrations of the dorsal and ventral layers of the LGN, PUL and PRT. A. Section at about A 8.0. There are two burn marks in the PUL, one in the dorsal layers of the LGN and one in layer B of the LGN. Both loci within the PUL produced responses upon stimulation of the ON. B. Section at about A 5.0. The burn mark is located at the dorsalmost aspect of the PRT. Magnification: about X 4.

LGN, PULVINAR, PRETECTUM

A



B

the LGN are rather large (in PUL as well), the center of the dorsal one would probably be at the border between laminae A and A1 or, perhaps, just below that border, in the dorsalmost part of lamina A1, and the center of the ventral burn mark would probably be in the center of lamina B. In Figure 29, it can be seen that sometimes the electrode tips within layer B encroached upon the incoming fibers of the OT. But, usually, this was not the case.

V. Summary

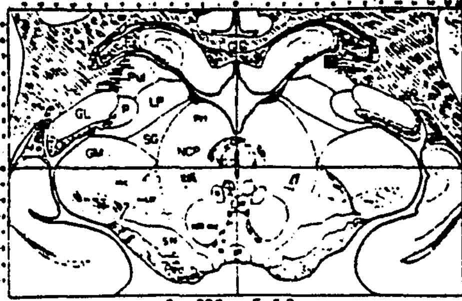
Table V presents the latency of all components of visual structures recorded from in the present study. Figure 30 presents schematic diagrams of typical responses recorded from all central visual structures upon ON stimulation in the present study, presented on the same time scale.

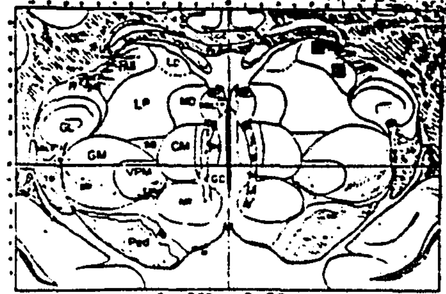
Of all the structures investigated (LAON, layers A, A1 and B of the LGN, SC, PRT, PUL and MRF), there was no response to ON stimulation only in the MRF. All other structures had responses of one to three components, with C1 of the LAON response having the shortest latency. Of the above structures, no response was elicited from the ON upon stimulation of only the MRF and PUL. In addition, while an ON response was recorded upon stimulation of the area about 2 mm below the SC, stimulation of the ON produced no response in this area.

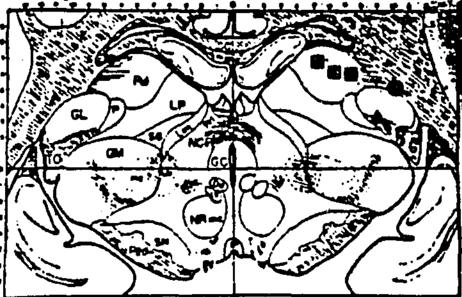
The responses of all structures, from which responses were elicited upon ON stimulation, had short latency first components, except PRT. The ON response to PRT stimulation did, however, have a short

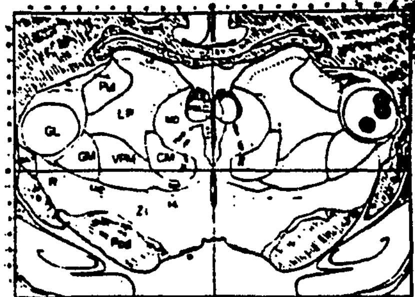
Figure 29. Series of schematic coronal sections, from the cat brain atlas of Jasper and Ajmone-Marsan (1954), upon which are plotted the loci within the dorsal and ventral layers of the LGN and PUL from which responses were elicited upon stimulation of the ON. Circles represent loci within layers A and A1 of the LGN, triangles represent loci within layer B of the LGN and squares represent loci within the PUL.

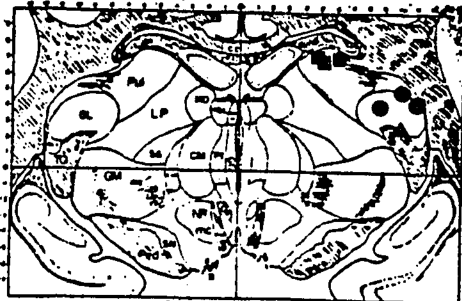
LGN PULVINAR











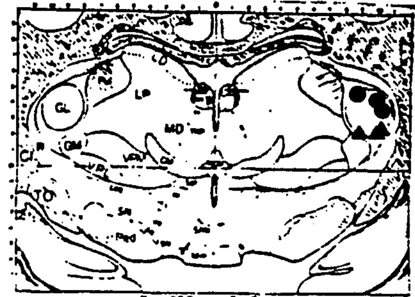
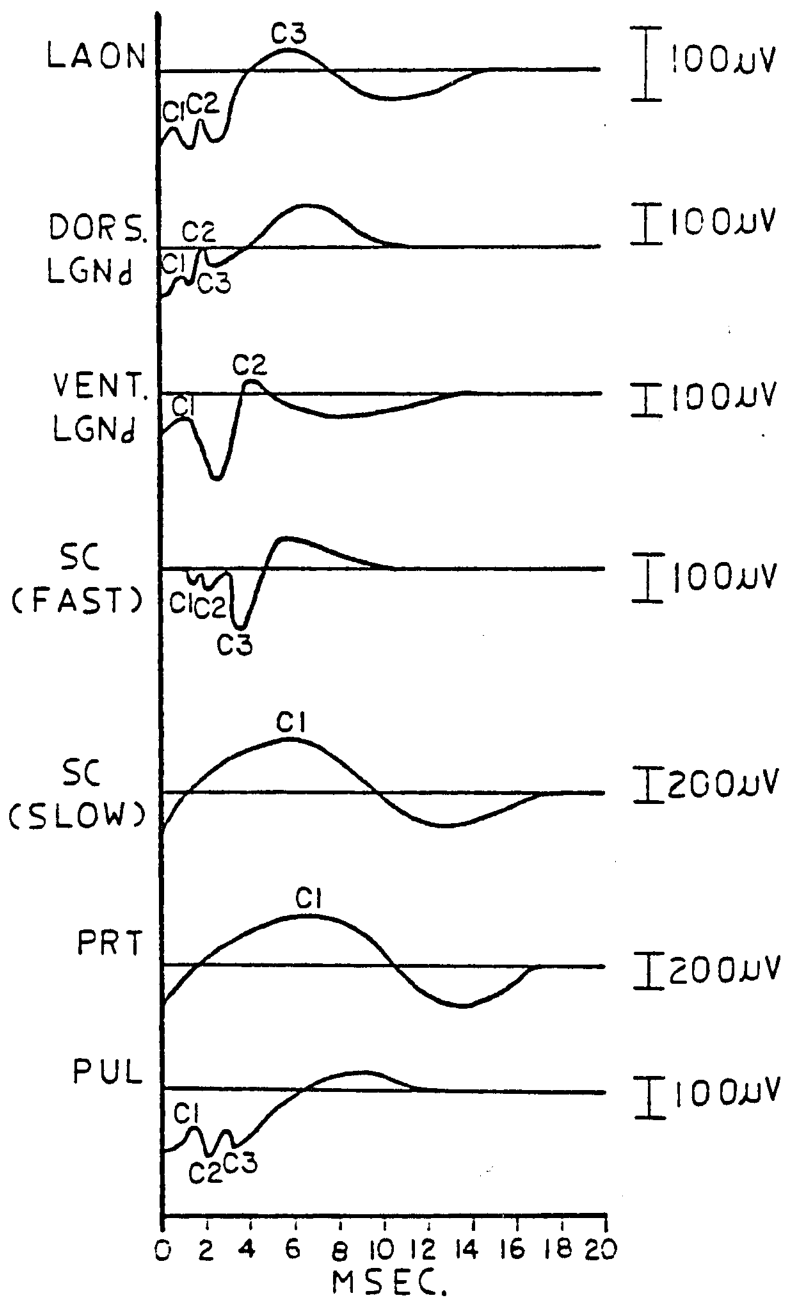


Table V. Median latency (in msec) of all components of responses recorded from central visual structures upon ON stimulation. Values in parentheses are ranges.

Structure	C1	C2	C3
Layers A and A1 of LGN	.8 (.6-.95)	1.8 (1.6-1.9)	5.6 (5.5-5.7)
Layer B of LGN	1.1 (.8-1.3)	2.0 (1.7-2.5)	2.5 (2.2-3.1)
"Slow" SC	6.0 (5.8-6.1)		
"Fast" SC	1.4 (1.0-1.6)	2.0 (1.4-2.5)	3.2 (1.9-5.8)
PRT	6.4 (6.2-6.5)		
PUL	1.5 (1.3-1.8)	2.4 (1.9-3.0)	3.5 (2.8-4.8)

Figure 30. Schematic diagrams of typical responses recorded from all central visual structures upon ON stimulation in the present study. Each component is labelled directly above or below its first inflection. Time scale at bottom represents latency of responses for the first inflection of each component. Polarity of the LAON response is the same as that of the other six responses presented, but is opposite to that of the LAON response presented in Figures 3, 4 and 5.


LAON
C3
C1 C2
100µV
DORS.
LGNd
C1
C2
C3
100µV
VENT.
LGNd
C1
C2
100µV
SC
(FAST)
C1 C2
C3
100µV
SC
(SLOW)
C1
200µV
PRT
C1
200µV
PUL
C1
C2 C3
100µV
0 2 4 6 8 10 12 14 16 18 20
MSEC.

latency component, as did the ON responses to stimulation of all other structures, except MRF, which elicited no ON response. In addition, short latency responses were recorded from the LAON upon stimulation of all other structures and vice versa.

Discussion

The main purpose of the present study was to investigate the nature of the optic nerve input to the LAON and to compare it with that of the ON fibers innervating other subcortical visual nuclei. Of prime importance in this comparison are conduction velocities of the various groups of ON fibers that directly innervate these structures. In addition, the present study sought to explore the possibility of centrifugal fibers coursing back into the ON, with special reference to the LAON as a source of such fibers. The results obtained for each structure will be discussed separately with regard to the above purposes.

I. ON input to LAON

In order to determine the conduction velocity of the ON fibers which directly innervate the LAON, it is necessary to ascertain whether each component of the LAON response to ON stimulation represents presynaptic, postsynaptic, orthodromic or antidromic activity. In order to do this, an analysis of the components of this response, along the lines of the analysis presented in Appendix 2, will now be undertaken.

The data presented in Table VII (Appendix 2) are actually the data presented in the Results section for the LAON response to ON stimulation and the ON response to LAON stimulation. The conclusions reached in Appendix 2 about the nature of the components presented in Table VII are, therefore, really conclusions about the

nature of the components of the LAON response to ON stimulation.

To review, it is concluded in Appendix 2 that C1 of the LAON response was a presynaptic orthodromic response, while C1 of the ON response was its antidromic counterpart. These conclusions were based on the fact that there is little difference in latency between these two C1s. C2 of the LAON response is concluded to be an intrinsic postsynaptic response of the LAON, set up by C1 of the LAON response, since C1 and C2 of the LAON response are time-locked, as demonstrated in Figure 5. C2 of the ON response to LAON stimulation represents orthodromic centrifugal activity going back into the optic nerve, but which crosses a synapse along the way. This must be so, since it could not represent an antidromic counterpart to C2 of the LAON response, since C2 of the LAON response is postsynaptic and, therefore, has no antidromic counterpart. In addition, C2 of the ON response must be postsynaptic, since it has no antidromic counterpart in the LAON response. C3 of the LAON response is an orthodromic presynaptic response, representing activity of a second group of ON fibers terminating in the LAON, and C3 of the ON response to LAON stimulation is its antidromic counterpart. The reasoning behind these conclusions is similar to that for the two C1s.

With a minimum conduction distance of 49 mm (see Results section), and with median latencies of .8 and 5.6 msec for C1 and C3 of the LAON response to ON stimulation respectively, the two groups of ON fibers represented by these two components have conduction velocities of 61 and 9 m/sec respectively. The value of 61 m/sec is considerably faster than that usually given for the ON axons of Y cells (30-40 m/sec), but 9 m/sec corresponds with the conduction

velocity of the axons of W cells (2-18 m/sec).

II. ON input to other subcortical nuclei

A. Layers A and A1 of LGN

Since the median latency of C1 of the response of layers A and A1 of the LGN to ON stimulation (1.1 msec) is essentially the same as that of the ON response to stimulation of these two layers (1.2 msec), it can be concluded, using the same reasoning that was used to analyse C1 of the LAON response, that C1 of the response of layers A and A1 represents a presynaptic response of direct retinal input and C1 of the ON response represents its antidromic counterpart. With a median latency of 1.1 msec and a minimum conduction distance of 38 mm (see Results section), the conduction velocity of the ON fibers which mediate C1 of the response of layers A and A1 is 35 m/sec, corresponding to that of axons of Y cells. This value of 35 m/sec is in basic agreement with those of Bishop (1953) (39 m/sec), Fukada et al (1966) (30-34 m/sec) and Hoffmann et al (1972) (33-44 m/sec).

The same conclusions can be drawn about C2 of the response of layers A and A1 to ON stimulation and C2 of the ON response to stimulation of these two layers, since their median latencies are essentially the same (2.0 and 1.9 msec respectively) and since the threshold of C1 of layers A and A1 (250 nanoC) is vastly different from that of C2 of this response (50 nanoC) (thereby eliminating the possibility that C2 is an intrinsic postsynaptic response of the nucleus, set up by C1). Thus, C2 of the response of layers A and A1 represents presynaptic input of ON fibers and C2 of the ON response

represents its antidromic counterpart. With a median latency of 2.0 msec and a minimum conduction distance of 38 mm (see Results section), the conduction velocity of the ON fibers responsible for C2 of the response of layers A and A1 is 19 m/sec, corresponding to that of axons of X cells (15-23 m/sec). This value of 19 m/sec is in basic agreement with those of Bishop (1953) (16 m/sec) and Hoffmann et al (1972) (19-24 m/sec).

Several facts indicate that C3 of the response of layers A and A1 is an intrinsic postsynaptic response initiated by C2. First, the threshold of C3 of this response (40 nanoC) is essentially the same as that of C2 (50 nanoC). An inspection of Figure 7C demonstrates that C2 and C3 drop out in unison. Second, C2 and C3 are time-locked. This is graphically demonstrated in Figure 8.

B. Layer B of LGN

According to the principles outlined in Appendix 2, the similarity in median latency between C1 of the response of layer B to ON stimulation (1.2 msec) and that of the ON response to stimulation of layer B (1.1 msec) indicates that C1 of the layer B response represents a presynaptic response of direct retinal input, and C1 of the ON response is its antidromic counterpart. With a median latency of 1.2 msec and a conduction distance of 36 mm (see Results section), the conduction velocity of the ON fibers responsible for the layer B response is 30 m/sec, corresponding to that of axons of Y cells.

With respect to C2 of the layer B response to ON stimulation, the difference in median latency between this component and C2 of the

ON response to layer B stimulation (4.0-3.8=.2 msec) is too small to be attributable to synaptic delay. Therefore, it must be concluded that C2 of the layer B response represents presynaptic activity, and C2 of the ON response represents its antidromic counterpart. With a median latency of 4.0 msec and a conduction distance of 36 mm (see Results section), the conduction velocity of the ON fibers responsible for C2 of the layer B response is 9 m/sec, corresponding to that of axons of W cells.

C. SC

Since the median latency of Cl of the "fast" SC response to ON stimulation (1.4 msec) is essentially the same as that of Cl of the ON response to SC stimulation (1.3 msec), it is concluded that Cl of the "fast" SC response represents presynaptic activity of direct retinal input, and Cl of the ON response is its antidromic counterpart. With a median latency of 1.4 msec and a minimum conduction distance of 45 mm (see Results section), the conduction velocity of the ON fibers which mediate Cl of the "fast" SC response is 32 m/sec, corresponding to that of axons of Y cells. This value of 32 m/sec is in basic agreement with those of Bishop et al (1969) (28-50 m/sec) and Hoffmann and Stone (1973) (35-45 m/sec). The later components (C2 and C3) of the "fast" SC response and the one component of the "slow" SC response have no counterparts in the ON response to SC stimulation. Thus, they must be postsynaptic responses.

D. PRT

Since there is no component in the PRT response to ON stimulation with a latency long enough to be considered an antidromic counterpart of C1 of the PRT response to ON stimulation, this component must be considered to be a postsynaptic response. The lack of a short latency response of the PRT to ON stimulation is particularly puzzling in light of the fact that the ON response to PRT stimulation consists of two short latency components. It is here hypothesized that the two short latency components recorded from the optic nerve upon stimulation of the PRT represent the antidromic counterparts of two orthodromic components of the PRT response to stimulation of th ON, which have not yet been described. These two orthodromic components would be mediated by ON axons with conduction velocities of 24 m/sec (corresponding to axons of X cells) and 36 m/sec (corresponding to axons of Y cells), based on their respective latencies of 1.8 and 1.2 msec and a minimum conduction distance of 43 mm (see Results section). Alternatively, these two ON components could represent antidromic activity passing through the PRT from some other structure(s). It is, of course, also possible that these two components recorded from the optic nerve are orthodromic (centrifugal), coming from some unknown source, but projected through the PRT. However, it seems parsimonious not to hypothesize a centrifugal response in the ON if there is an alternative interpretation, as there is here.

E. PUL

Although a direct retinal projection to the PUL has recently been demonstrated anatomically in the cat, nevertheless, no antidromic response was noted when recording from the ON upon PUL stimulation in the present study. However, the area of termination of ON fibers within the PUL consists of a thin sheet of cells along the lateral border of the nucleus, just dorsomedial to the LGN (Itoh et al, 1979). Thus, only a very small area of the PUL consists of cells receiving ON fibers. Since the PUL electrode was not located at this extreme edge of the PUL right next to the LGN in the present study, it is not surprising that no response was observed in the records from the ON upon stimulation of the PUL.

Upon ON stimulation, the latency of the first component of the PUL response was 1.5 msec and that of layer B of the LGN was 1.2 msec. The difference of .3 msec renders unlikely the possibility that the first comppnent of the PUL response could be a postsynaptic response with the synapse being in layer B of the LGN. This difference in latencies is probably not great enough to account for both the synaptic delay within layer B and the conduction time from layer B to the PUL. So, if the first component of the PUL response to ON stimulation represents direct retinal input, the ON fibers mediatthis component would have a conduction velocity (with the conduction distance equal to, let us say, about 43 mm) of about 29 m/sec. Alternatively, the PUL response to ON stimulation could be a postsynaptic response, with the synapse relatively far away from the electrode, like along the lateral edge of the PUL, where ON fibers

have been found to terminate. Pursuing this alternative, if we allow .5 msec for synaptic delay, the conduction velocity of the ON fibers innervating the PUL would be about 43 m/sec, corresponding to that of axons of Y cells.

F. Summary and Comments

The ON was found to be composed of the following groups of fibers:

Terminating in the LAON, two groups conducting at 61 and 9 m/sec.

Terminating in layers A and A1 of the LGN, two groups conducting at 35 and 19 m/sec.

Terminating in layer B of the LGN, two groups conducting at 30 and 9 m/sec.

Terminating in the SC, one group conducting at 32 m/sec.

Terminating in the PRT, two hypothesized groups conducting at 36 and 24 m/sec.

Terminating in the PUL, perhaps one group conducting at 43 m/sec.

In comparing the LAON with other subcortical visual structures, two results of the present study stand out. The first is that the value of 61 m/sec for the conduction velocity of ON fibers innervating the LAON is faster than that for any of the other structures studied. This value is much faster than those usually given for axons of Y cells (30-40 m/sec), which have been thought to be the fastest conducting fibers in the visual system. The second is that

the LAON sends a centrifugal projection back through the ON, after synapsing at an unknown site. No other visual structure was found to project back into the ON (but see below). Thus, the nature of the relations between the LAON and ON is very different from those between the other subcortical visual nuclei and the ON.

III. Centrifugal input to the ON

Two indirect sources of centrifugal input to the ON have been found in the present study, namely the LAON and the area about 2 mm below the SC. The evidence that the responses of the ON upon stimulation of these two structures really do contain centrifugal activity is as follows. With regard to the area about 2 mm below the SC, since this area does not, itself, respond to ON stimulation, there is no retinal projection to this area. So, the one component ON response, upon stimulation of this area, cannot be an antidromic response going along non-existent ON fibers. Thus, it must be an orthodromic response. In addition, the ON response to stimulation of this area about 2 mm below the SC cannot be a direct projection; there must be at least one intervening synapse. Such a synapse must be present, for if it were not, a response would be seen in this area upon stimulation of the ON - it would be the antidromic counterpart of the ON response to stimulation in this area. Since no response is seen from this area upon ON stimulation, such an intervening synapse must be present.

The evidence that C2 of the ON response to LAON stimulation also represents centrifugal activity, but also with an intervening

synapse, is of a similar nature. It has already been concluded that C2 of the LAON response to ON stimulation is set up by C1 of the same response, and does not, therefore, represent activity of fibers of retinal origin. Thus, C2 of the ON response to LAON stimulation could not be the antidromic counterpart of C2 of the LAON response, and C2 of the LAON response could not be the antidromic counterpart of C2 of the ON response. So, C2 of the ON response must be orthodromic. And, C2 of the ON response must be postsynaptic, since there is no component in the LAON response to ON stimulation that could be interpreted as the antidromic counterpart of C2 of the ON response.

The waveform and amplitude of C2 of the ON response to LAON stimulation (a centrifugal component) are very similar to the waveform and amplitude of the ON response to stimulation of the area about 2 mm below the SC (the other centrifugal component) (compare C2 in Figure 6A, B and C with C1 in Figure 18A, B and C respectively). Therefore, it is likely that both these structures (the LAON and the area about 2 mm below the SC) project to a single other structure, which is the source of direct centrifugal input to the retina.

While there have been scattered reports of the presence of centrifugal fibers in the optic nerve of mammals, it is generally considered that it is only in the pigeon that such fibers have been definitively shown to exist, with their source being the isthmo-optic nucleus. Ogden (1968) assigs to these fibers in the pigeon the function of inhibiting light-evoked oscillatory activity in the retina. Functions assigned to such fibers in mammals are still speculative. The importance of the results of the present study lies in their making possible future studies on the functional signifi-

cance of centrifugal input to the ON of mammals, since the present study has located two reliable (though indirect) loci from which such centrifugal input to the ON can be activated.

IV. W, X, Y

In recent years, much effort has been devoted to classifying unit discharges in the optic nerve on the basis of receptive field properties and axonal conduction velocities, as discussed in the Introduction. From this has come the W, X, Y classification of retinal ganglion cells. Although no units were investigated in the present study, axonal conduction velocities were. Thus, it is important to relate the findings of the present study to those of recent studies involving the W, X, Y classification.

Based on conduction velocities obtained in the present study, it is concluded that axons of Y ganglion cells may innervate layers A, A1 and B of the LGN, the SC, PRT, PUL and (perhaps) the LAON. Axons of X ganglion cells may innervate layers A and A1 of the LGN and the PRT, and axons of W ganglion cells may innervate the LAON and layer B of the LGN.

Whether the retinal ganglion cells from which all these axons originate possess the receptive field characteristics typical of W, X and Y cells is presently unknown, since no units were investigated in the present study. However, if they do, they allow certain hypotheses to be formulated. Thus, the results of the present study, coupled with those of other studies, indicate that all subcortical visual nuclei receive fast conducting (Y type) ON fibers. Since

Y type ganglion cells are known to be particularly sensitive to the sudden onset or offset of light, all subcortical visual centers receive a very quick neural message as soon as there is a sudden change in light conditions at the retina (such as when a big predator or a small prey crosses the animal's field of vision). The Y type input may have an alerting function. Such Y type input lets the visual system know that "something out there has changed", and lets it know very quickly, so that further processing can be prepared for and undertaken.

The further processing comes with the arrival of X type input a little later than the Y type input, due to the slower conduction velocity of X type ON axons. Thus, the Y input has alerted the visual system to a change "out there" and the X input will now describe the nature of the change; it will give the details. That it can give the details is implied by Fukuda and Stone (1974), who feel that the X type retinal ganglion cells play a part in high resolution vision, due to the small size of their receptive fields and their location in the area centralis.

Some W type retinal ganglion cells have response characteristics similar to those of X cells and others have response characteristics similar to those of Y cells (Stone and Fukuda, 1974). Thus, the slower W cell input to subcortical visual nuclei could be a means of keeping the rest of the brain informed about what the visual system is currently "working on" (which is X and Y input). That is, W input could give approximately the same information as X and Y input, but it would give this information later than the X and Y input, and it would give it, ultimately, to parts of the brain other

than the subcortical visual nuclei. This could be accomplished by W input reaching, say, the MRF. The present study has shown that the LAON, which does receive W input, does, indeed, project to the MRF. Thus, Y input alerts the visual system to a sudden change in the animal's visual world, X input describes the nature of the change, and W input allows the rest of the brain also to know what the visual system is currently dealing with.

Appendix 1

Calculation of Distance Traversed by ON-OT Fibers in going to LAON, SC and PRT

What was calculated was the distance from a point 1 mm below the entrance of the OT fibers into the most ventral aspect of the LGN, within the OT fibers, to a point within the SC, PRT and LAON on the same side of the brain. This value could then be added to the value obtained for the length of the ON-OT to the most ventral aspect of the LGN (minus 1 mm). A point 1 mm below the entrance of the OT fibers into layer B of the LGN was chosen, as opposed to the actual point of entrance of these fibers, because the OT fibers which go to the SC, PRT and LAON bypass the LGN by turning medially just under the nucleus. Those OT fibers at the point of entrance to layer B are entering the LGN, and are not coursing toward the SC, PRT and LAON. In addition, the anteroposterior level of this point 1 mm below the entrance of the OT fibers into layer B was chosen so as to be the most anterior level of the LGN where some of the fibers of the entering OT are seen to start to course medially under the nucleus. The location of each endpoint within the SC and PRT to which measurements were made was chosen so as to be in the approximate center of the electrode tip loci from which data were obtained, as seen in the histological sections of the present study.

It was not possible to do the same thing with the LAON endpoint, since so few plates containing this nucleus are presented in cat brain atlases. So, the endpoint within the LAON was chosen so as

to be in the approximate center of the nucleus as presented in the given atlases. When as many as two plates containing the LAON were presented in an atlas, the endpoint used was in the center of the nucleus in the location closest to that of the approximate center of the electrode tip loci from which data were obtained, as seen in the histological sections of the present study. However, the course of the ON fibers which go past the LGN and terminate in the LAON consists of a dorsal branch - ascending within the brachium of the superior colliculus (BSC) - and a ventral branch - descending from the BSC to the ventrally placed LAON. In order to measure more accurately the distance traversed by these fibers, first the distance from just below the LGN to the BSC was measured, and then the distance from the BSC to the LAON was measured.

The distance traversed by those OT fibers entering the ventralmost aspect of the LGN and terminating in the two dorsal layers was also measured to the approximate center of the electrode tip loci from which data were obtained, as seen in the histological sections of the present study. The coordinates of the points from and to which measurements were made in each atlas are presented in Table VI.

In order to explain exactly how the Pythagorean theorem was used to make these calculations, one such calculation shall be described in detail. From Table VI, we see that the coordinates from the atlas of Jasper and Ajmone-Marsan (1954) for 1 mm below the ventralmost LGN were A 6.5, L 10.5, H 1.0, while those for the SC were A 2.0, L 2.5, H 3.5. On the plate labelled A 6.5 in this atlas, a line joining the point H 1.0, L 10.5 to the point at H 1.0, L 2.5 (a distance of 8 mm) forms a right triangle with a line joining the

Table VI. Coordinates from four stereotaxic atlases of the cat brain used to calculate the minimum length of the OT fibers from a point 1 mm below the ventralmost LGN to their terminations within the dorsal layers of the LGN, SC PRT and LAON. Coordinates for the BSC are given since they were used in determining the minimum length of the ON-OT to the LAON. Since the atlas of Fifkova and Marsala (1967) presents just line drawings and no photographs of actual sections, and since they do not label the LAON, it was impossible to determine the length of the OT fibers to the LAON based on this atlas. So, to present coordinates for the BSC from this atlas would be superfluous.

Cat Brain Atlas	Entrance of OT fibers into ventral-most LGN			Dorsal layers of LGN			1 mm below ventralmost LGN			PRT			SC			BSC			LAON		
	A	L	H	A	L	H	A	L	H	A	L	H	A	L	H	A	L	H	A	L	H
Snider and Niemer (1961)	6.0	11.5	3.0	6.0	11.5	5.5	6.0	11.5	2.0	4.5	2.5	3.5	2.0	2.5	4.5	4.0	5.0	5.0	2.5	7.5	-3.0
Fifkova and Marsala (1967)	6.0	11.0	4.0	6.0	11.0	6.5	6.0	11.0	3.0	4.5	3.0	3.0	2.0	2.5	4.0				*	*	*
Berman (1968)	6.4	10.5	3.0	6.4	10.5	4.5	6.4	10.5	2.0	5.2	2.5	3.5	2.5	2.5	4.5	5.2	4.5	5.0	3.3	6.8	-2.0
Jasper and Ajmone-Marsan (1954)	6.5	10.5	2.0	6.5	10.5	4.4	6.5	10.5	1.0	4.0	3.5	3.0	2.0	2.5	3.5	4.0	6.0	4.0	4.0	7.0	-4.0

point at H 3.5, L 2.5 to the point at H 1.0, L 2.5 (a distance of 2.5 mm). A line from H 3.5, L 2.5 to H 1.0, L 10.5 completes a right triangle, forming its hypoteneuse. The length of this hypoteneuse is, of course, the square root of (8.0 squared + 2.5 squared), which equals 8.4 mm, which is the distance from A 6.5, L 10.5, H 1.0 to A 6.5, L 2.5, H 3.5. An imaginary line joining the point A 6.5, L 2.5, H 3.5 to the point A 2.0, L 2.5, H 3.5 (a distance of 4.5 mm) forms a right angle with the line joining the point A 6.5, L 10.5, H 1.0 to the point A 6.5, L 2.5, H 3.5 (a distance just calculated to 8.4 mm). An imaginary line from A 2.0, L 2.5, H 3.5 to A 6.5, L 10.5, H 1.0 completes this right triangle, forming its hypoteneuse. The length of this hypoteneuse is the square root of (8.4 squared + 4.5 squared), which equals 9.5 mm, which is the shortest distance between A 6.5, L 10.5, H 1.0 (the point 1 mm below the ventralmost LGN) to A 2.0, L 2.5, H 3.5 (the chosen point within the SC). This procedure was followed for calculating all other distances. In the case of the LAON, this procedure was followed twice - once to calculate the distance from 1 mm below the ventralmost LGN to the BSC and again, to calculate the distance from the BSC to the LAON.

Appendix 2

Determination of Presynaptic, Postsynaptic, Antidromic and Orthodromic Activity

If one stimulated the ON (point 1 in Figure 31) and recorded from a central structure, which shall be called here "structure A", and then stimulated structure A and recorded from the ON in, say, 30 cats, and if one recorded data such as those presented in Table VII, several possibilities as to the nature of the activity responsible for these components might seem plausible. Starting with C1 of the response of structure A, the first question to arise might be: does C1 represent presynaptic or postsynaptic activity? That is, was C1 recorded from point 4 or points 8 or 9 in Figure 31? (The possibility that C1 was recorded from point 6 will be held in abeyance for now.) If C1 represented postsynaptic activity (from points 8 or 9), its .8 msec latency would include, let us say, about .4 msec, which would be required to cross the synapse labelled 5 in Figure 31. Thus, the presynaptic latency of C1 would be .4 msec. Such a latency would probably imply a conduction velocity much faster than any presently known for the visual system. But, that does not necessarily rule out such a possibility. What does rule out the possibility of C1 being a postsynaptic response is the .8 msec latency of C1 of the ON response upon stimulation of structure A (see Table VII). On the assumption that C1 of the ON response is the antidromic counterpart to C1 of the structure A response (other assumptions will be considered shortly), since this antidromic response had to

Figure 31. Schematic diagram of possible conduction paths from the ON to a hypothetical central structure A and from this structure back through the ON. E = electrode; S = stump of sclera. The thick double lines next to the sclera indicate that the retina has been removed.

1 = point of stimulation and recording from ON fibers. The oval band indicates that all the fibers it encircles are in the ON

2, 5, 7, 10, 19 = synapses

3, 8, 11 = somas

12, 17 = groups of centripetal ON fibers

13, 16 = groups of centrifugal ON fibers

15, 18 = groups of fibers outside of ON

4, 6, 20 = axonal terminations at synapses

9 = postsynaptic locus within structure A

14 = point on centrifugal ON fibers 13 just peripheral to their soma of origin

21 = indeterminate point along non-ON fibers entering structure A

Dotted lines indicate the parts of centrifugal fibers which were destroyed upon removal of the retina.

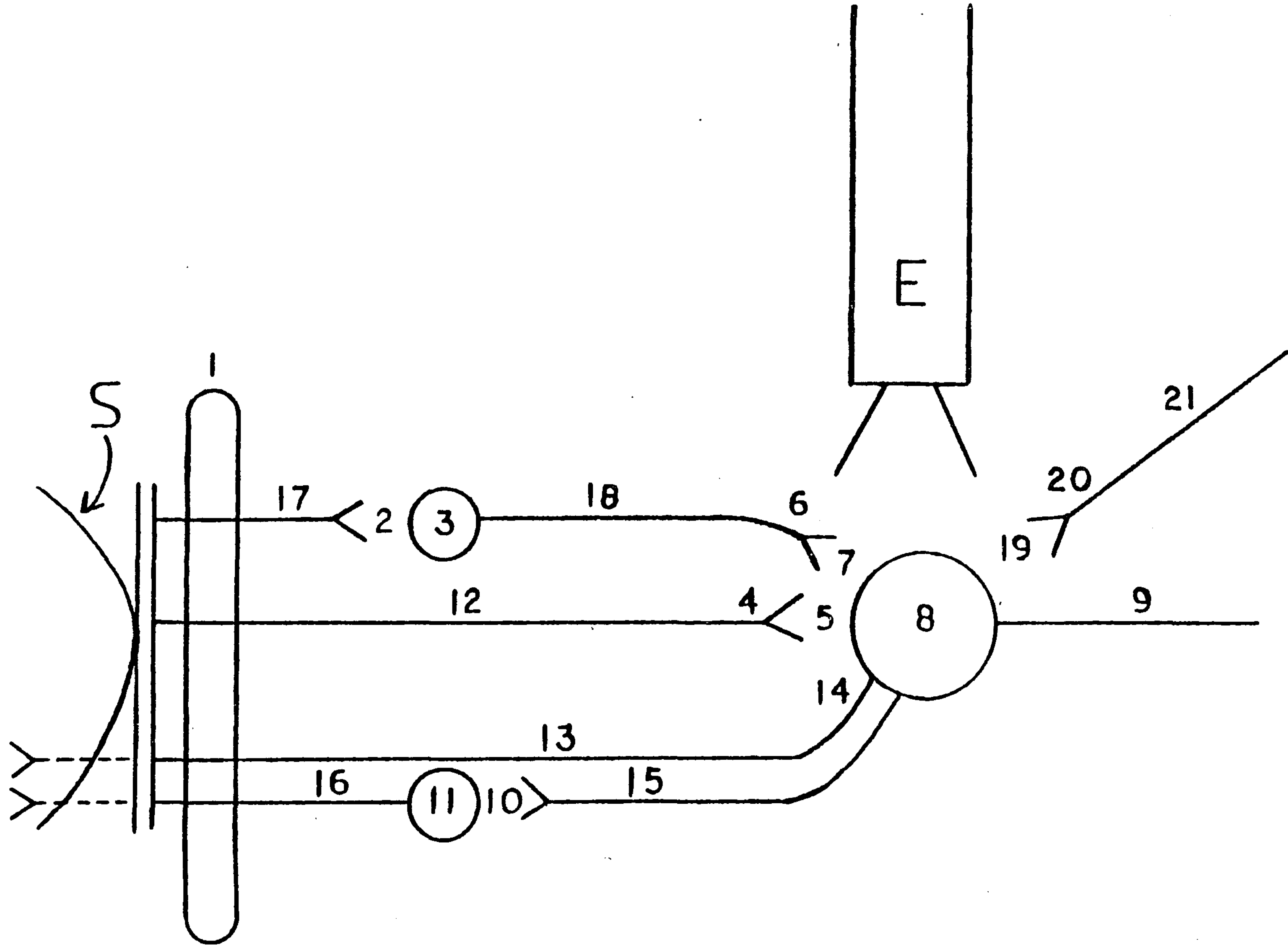

E
1
S
17
2
3
18
6
7
21
20
19
12
4
5
8
9
14
13
16
11
10
15

Table VII. Hypothetical median latencies (in msec) and thresholds (in nanoC) of the three components of a response recorded from a central structures ("structure A") upon ON stimulation and of the ON response to stimulation of the hypothetical structure A. The arrow indicates the direction of stimulation-recording.

		C1		C2		C3	
		Latency	Threshold	Latency	Threshold	Latency	Threshold
ON	Structure A	.8	250	1.8	250	5.6	100
Structure A	ON	.8	200	2.1	250	5.5	100

start at point 4 and not postsynaptically at point 8 or 9 (since an antidromic response will not cross a synapse), one would expect the response recorded at point 4 upon ON stimulation to have about the same latency (.8 msec). So, on this basis, it can be concluded that Cl of the response of structure A must be presynaptic and that Cl of the ON response is its antidromic counterpart.

The objection might be raised that Cl of the ON response might represent orthodromic centrifugal activity initiated at point 4, which crossed synapse 5 to soma 8 and went back through the ON orthodromically, along the ON fibers labelled 13. But, if this were so, if we again allow .4 msec for crossing synapse 5 from point 4, and subtract this .4 msec from the .8 msec latency of Cl of the ON response, we are left with .4 msec for this activity to go down the fibers labelled 13 within the ON from soma 8. This would not seem to be an impossibility, though again, it would imply an extremely fast conduction velocity. But, what does make this rather unlikely is that if Cl of the ON response did represent such orthodromic activity, one would expect to see a component in the records taken from structure A with a latency of about .4 msec, which would represent the antidromic counterpart of an orthodromic Cl of the ON response. It would be recorded from about point 14. Since such a component is not seen in the records taken from structure A, it can be concluded that Cl of the ON response cannot represent orthodromic centrifugal activity initiated at point 4, crossing synapse 5 to soma 8 and going back in the ON along ON fibers 13. The same reasoning also explains why Cl of the structure A response could not be coming from point 6 or 8 and going orthodromically back along

ON fibers 13, or fibers 15 and ON fibers 16.

The objection could be raised that C1 of the ON response represents orthodromic centrifugal activity initiated at soma 8 and going along fibers 15, crossing synapse 10 and soma 11 and continuing along ON fibers 16. If this were so, C1 of the structure A response would be antidromic and would be recorded from point 4 (since it would not cross synapse 5, being antidromic). However, it can be shown that C1 of the structure A response cannot be antidromic. The values in Table VII represent medians. The latency of C1 of the structure A response was not .8 msec in every cat, nor was the latency of C2 of this response 1.8 msec in every cat. If it can be shown that these two components (C1 and C2 of the structure A response to ON stimulation) are time-locked, it would indicate that there is a causal relationship between them; that is, the activity of C1 causes or triggers the activity of C2. If this were so, the usual interpretation would be that C1 was presynaptic and C2 postsynaptic. However, if C1 of the structure A response represented antidromic activity, it could not trigger C2, and certainly could not cross a synapse. So, if when the latency of C1 of the structure A response was sometimes, say, 1.1 msec (due to slight variation from cat to cat), and not .8 msec (a difference of .3 msec), the latency of C2 was also shifted over by .3 msec to a value of 2.1 msec, a causal relationship between C1 and C2 of the structure A response would be established, which would mean that C1 of this response could not be antidromic, and so C1 of the ON response could not represent orthodromic centrifugal activity initiated at soma 8 and going along fibers 15 and ON fibers 16. The

fact that the thresholds of C1 and C2 of the structure A response are the same (see Table VII) lends support to the existence of a causal relationship between C1 and C2, but, by itself, would not be convincing. The time-locking of C1 and C2 of the structure A response is most important to this argument. In summary, it has been shown that, given the data in Table VII and certain other information, C1 of the structure A response must represent presynaptic orthodromic activity, recorded at about point 4 in Figure 31, while C1 of the ON response must represent antidromic activity recorded at point 1 in Figure 31.

With regard to C2 of the structure A response, since it has already been concluded that it represents activity caused by C1, we can exclude the possibility that it represents activity conveyed to structure A by ON fibers conducting slower than those conducting the activity represented by C1 to structure A. C2 represents intrinsic activity of structure A itself. C2 of the ON response must, therefore, represent orthodromic centrifugal activity initiated at soma 8 or someplace else within structure A, going along fibers 15, crossing synapse 10 to soma 11 and continuing along ON fibers 16. It is because there is a synapse (10) between fibers 15 and ON fibers 16 that C2 of the structure A response cannot be an antidromic counterpart to C2 of the ON response, since an antidromic response will not cross a synapse. Also, C2 of the structure A response could not be an antidromic response, since it has already been shown that it is caused by C1 of the structure A response.

Notice that the conclusion that C2 of the structure A response is an intrinsic response caused by C1 would not be contradicted

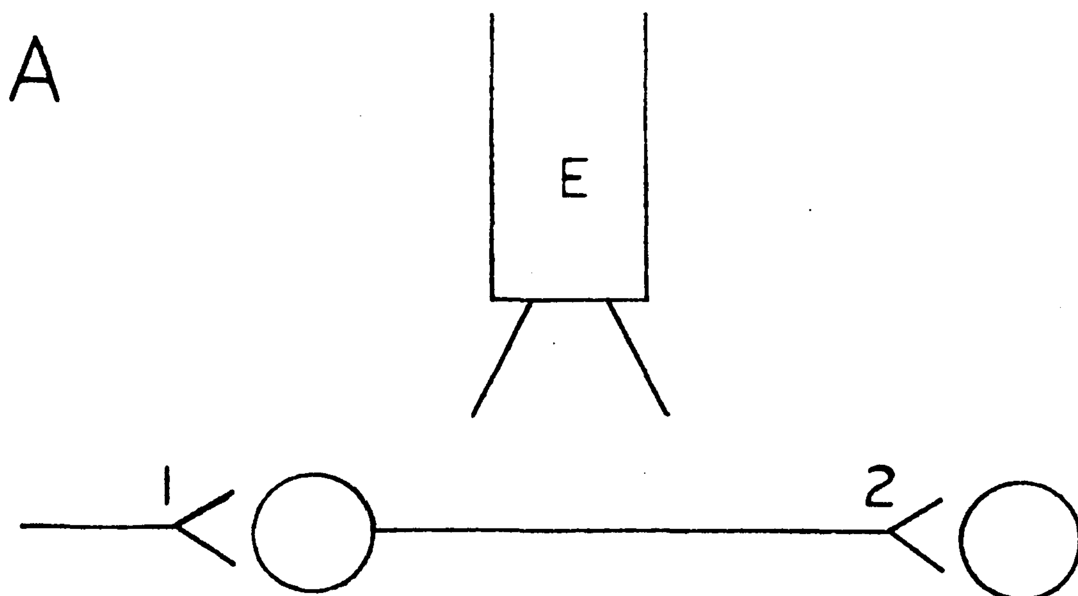
if it should occasionally happen that C2 of the structure A response were present in the recording but C1 of this response were not. It is possible that the spatial relationships of the cells of structure A are such that the parts of structure A from which C1 and C2 are recorded are situated far enough apart so that only if the recording electrode were approximately half way between them (as in Figure 32A) would it record both components. If the recording electrode were very close to the part of structure A from which C2 is recorded, and, therfore, relatively far from that part from which C1 is recorded (as in Figure 32B), only C2 would be picked up. C1 would have occurred, and caused C2, but the recording electrode would have been too far away to pick up C1.

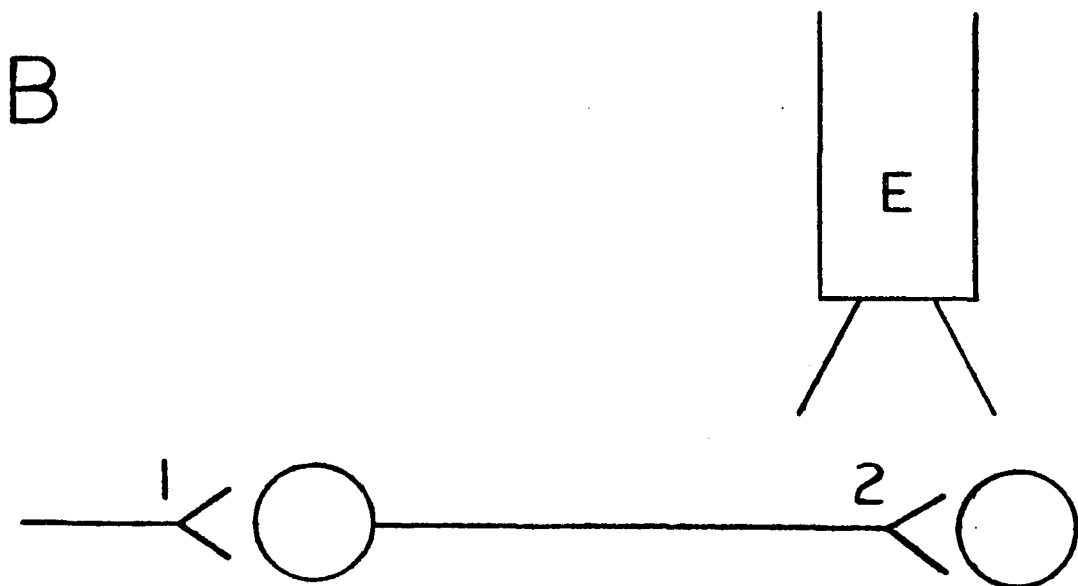
With respect to C3 of the structure A response to ON stimulation, if we assume that the latency of this component did not shift to 5.9 msec on the occasions when the latencies of C1 and C2 shifted to 1.1 and 2.1 msec respectively, but remained at about 5.6 msec, it can be concluded that C3 is not initiated by C1 or C2. Thus, it represents independent ON input to structure A. Given the 5.5 msec latency of C3 of the ON response, and, on the assumption that this (C3 of the ON response) is an antidromic response (other assumptions will be considered shortly), C3 of the structure A response must be presynaptic. This is so because if C3 of the structure A response were postsynaptic, its antidromic counterpart (C3 of the ON response) would have to have a latency shorter, by about .4 msec, than that of C3 of the structure A response, since C3 of the ON response, being an antidromic component, would not cross the synapse that C3 of the structure A response did. Since this .4 msec difference

Figure 32. Schematic diagram of hypothetical spatial relationship between some cells in structure A. E. -- recording electrode; 1 -- presynaptic fibers from which C1 of the structure A response would be recorded; 2 -- indeterminate postsynaptic locus, within structure A, from which C2 of the structure A response would be recorded.

A. Electrode tips are equidistant between the part of structure A responsible for C1 of the structure A response and that responsible for C2 of this response. Both C1 and C2 would be picked up by this electrode.

B. Electrode tips are close to the part of structure A responsible for C2 of the structure A response, but far from that responsible for C1 of this response. Only C2 would be picked up by the electrode.


A
E
1
2


B
E
1
2

between the latencies of the two C3s is not present, it must be concluded that C3 of the structure A response is presynaptic. The .1 msec difference that does exist between the two C3s could not be considered to be long enough to represent synaptic delay.

Could C3 of the ON response be an orthodromic (centrifugal) response? That is, if C3 of the structure A response represented orthodromic activity recorded from point 4 (Figure 31), could the activity responsible for C3 of the ON response go back into the ON along fibers 13, or even fibers 15 and 16? Yes it could, but if it did go back to the ON along fibers 15 across synapse 10 and then along fibers 16, it would have no antidromic counterpart recordable in structure A, since an antidromic counterpart would not cross synapse 10. Thus, we would have to assume that C3 of the structure A response could not be the antidromic counterpart of C3 of the ON response. C3 of the structure A response would still have to be orthodromic. Given the fact that C3 of the structure A response would still have to orthodromic, it can be seen that C3 of the ON response would have to represent not only orthodromic activity which crossed synapse 10, but also antidromic activity - the antidromic counterpart of C3 of the structure A response - going back into the ON along fibers 12. While it is possible for two different responses to get to the same site of recording at exactly the same time, and, therefore, appear to be only one response, one would expect that sometimes, perhaps frequently, the slight deviations from median latency that would occur in both these components would not exactly cancel each other out, and so two components would then be seen. For example, on occasion, the latency of the antidromic counterpart

of C3 of the structure A response might be 5.7 msec, while the latency of the orthodromic response going along fibers 15 and 16 might be 5.4 msec. On this occasion, two components - not one - would be easily differentiated. On the assumption that two such components were not seen upon recording from the ON, it must be concluded that C3 of the ON response could not be orthodromic, going along fibers 15, crossing synapse 10 and then continuing along fibers 16.

The same reasoning eliminates the possibility that C3 of the ON response could be orthodromic, conducted along fibers 13, on the assumption that C3 of the structure A response represented orthodromic activity going along fibers 12 plus antidromic activity going along fibers 13 - the antidromic counterpart of the orthodromic C3 of the ON response, also conducted along fibers 13. But, could C3 of the structure A response really be the antidromic counterpart of the orthodromic C3 of the ON response? Probably not, for if this were so, one would expect the latency of C3 of the ON response to be longer, by about .4 msec or more, occasionally, since stimulation within structure A would not be expected to always occur right at soma 8 or point 14; it could occur a synapse or more away, like at point 20 or even point 21. If such an occasional long latency C3 were not seen in the response of the ON, one could rule out the possibility that this C3 was orthodromic, going along fibers 13 back into the ON. So, C3 of the ON response must be an antidromic response. This rules out the possibility that C3 of the structure A response could be recorded at point 6, having gone along fibers 17, crossing synapse 2 and having continued along fibers 18, for such a response would have no antidromic counterpart (since the activity

represented by such a counterpart could not cross synapse 2). Yet, we know that such antidromic activity is present in the ON response, represented by C3.

In summary, it has been shown, based on Figure 31, the data presented in Table VII and certain other information, that C1 and C3 of the structure A response represent independent, orthodromic activity, recorded presynaptically, and C1 and C3 of the ON response represent their antidromic counterparts respectively. C2 of the structure A response represents activity intrinsic to structure A, initiated by the activity represented by C1 of the structure A response. C2 of the ON response represents orthodromic (centrifugal) postsynaptic activity.

Appendix 3

Polarity

Since all recording in the present study was bipolar, there was no reference on an electrically inactive substance by means of which one could determine absolute polarity of recorded responses. However, relative polarity (of one response compared to any other response) could be, and was, determined by noting the polarity of the biphasic shock artifact. Thus, if the polarity of the shock artifact in two different responses was the same, the polarity of those two responses was also the same. If the polarity of the shock artifact were reversed, the polarity of the response would also be reversed.

The polarity of all responses in the present study was the same, except for that of the LAON response to ON stimulation. This response, as presented in Figures 3, 4 and 5 has reversed polarity relative to all other responses.

References

Altman, J. Some fiber projections to the superior colliculus in the cat. J. Comp. Neurol., 1962, 119: 77-96.

Altman, J. and Malis, L.I. An electrophysiological study of the superior colliculus and visual cortex. Exp. Neurol. 1962, 5: 233-249.

Barris, W.R., Ingram, W.R. and Ranson, S.W. Optic connections of the diencephalon and midbrain of the cat. J. Comp. Neurol. 1935, 62: 117-153.

Berman, A.L. The Brain Stem of the Cat. A Cytoarchitectonic Atlas with Stereotaxic Coordinates. Madison, Wisconsin: Univ. of Wisconsin Press, 1968.

Bishop, P.O. Synaptic transmission. An analysis of the electrical activity of the lateral geniculate nucleus in the cat after optic nerve stimulation. Proc. Roy. Soc. B. 1953, 141: 362-392.

Bishop, G.H. and Clare, M.H. Organization and distribution of fibers in the optic tract of the cat. J. Comp. Neurol. 1955, 103: 269-304.

Bishop, G.H., Clare, M.H. and Landau, W.M. Further analysis of fiber groups in the optic tract of the cat. Exp. Neurol. 1969, 24: 386-399.

Brindley, G.S. and Hamasaki, D.I. Histological evidence against the view that the cat's optic nerve contains centrifugal fibres. J. Physiol. 1966, 184: 444-449.

Chalupa, L.M., Anchel, H. and Lindsley, D.B. Visual input to the pulvinar via lateral geniculate, superior colliculus and visual cortex. Exp. Neurol. 1972, 36: 449-462.

Clare, M.H., Landau, W.M. and Bishop, G.H. The relationship of optic nerve fiber groups activated by electrical stimulation to the consequent central postsynaptic events. Exp. Neurol. 1969, 24: 400-420.

Cleland, B.G., Levick, W.R., Morstyn, R. and Wagner, H.J. Lateral geniculate relay of slowly conducting retinal afferents to cat visual cortex. J. Physiol. 1976, 225: 299-320.

Cleland, B.G., Morstyn, R., Wagner, H.G. and Levick, W.R. Long-latency retinal input to lateral geniculate neurones of the cat. Brain Res. 1975, 91: 306-310.

Cowan, W.M., Adamson, L. and Powell, T.P.S. An experimental study of the avian visual system. J. Anat. 1961, 95: 545-563.

Dodt, E. Geschwindigkeit der Nervenleitung innerhalb der Netzhaut. Experientia, 1956, 12: 34-35.

Erlanger, J. and Gasser, H.S. Electrical Signs of Nervous Activity. Philadelphia: Univ. of Pennsylvania Press, 1937.

Fifkova, E. and Marsala, J. Stereotaxic atlases for the cat, rabbit, and rat. In: Electrophysiological Methods in Biological Research, J. Bures, M. Petran and J. Zachar (eds.), New York: Academic Press, 1967, 653-731.

Fillenz, M. and Glees, P. Degeneration of optic nerve fibres in the cat. J. Physiol. 1961, 158: 18P.

Fukada, Y. Receptive field organization of cat optic nerve fibres with special reference to conduction velocity. Vision Res. 1971, 11: 209-226.

Fukada, Y., Motokawa, K., Norton, A.C and Tasaki, Y. Functional significance of conduction velocity in the transfer of flicker information in the optic nerve of the cat. J. Neurophysiol. 1966, 29: 698-714.

Fukuda, Y. and Stone, J. Retinal distribution and central projections of Y-, X-, and W- cells in the cat's retina. J. Neurophysiol. 1974, 37: 749-772.

Garey, L.J., Jones, E.G. and Powell, T.P.S. Interrelationships of striate and extrastriate cortex with the primary relay sites of the visual pathway. J. Neurol. Neurosurg. Psychiat. 1968, 31: 135-157.

Gorikov, N.G. Centrifugal and centripetal fibers composing the optic nerves. Byull. Eksp. Biol. Med. 1969, 68: 101-105.

Granit, R. Centrifugal and antidromic effects on ganglion cells of retina. J. Neurophysiol. 1955, 18: 388-411.

Hoffmann, K.-P. The retinal input to the superior colliculus in the cat. Invest. Ophthal. 1972, 11: 467-473.

Hoffmann, K.-P. Conduction velocity in pathways from retina to superior colliculus in the cat: A correlation with receptive-field properties. J. Neurophysiol. 1973, 36: 409-424.

Hoffmann, K.-P., Stone, J. and Sherman, S.M. Relay of receptive-field properties in dorsal lateral geniculate nucleus of the cat. J. Neurophysiol. 1972, 35: 518-531.

Itoh, K., Mizuno, N., Sugimoto, T., Nomura, S., Nakamura, Y. and Konishi, A. A cerebello-pulvino-cortical and a retino-pulvino-cortical pathways in the cat as revealed by the use of the anterograde and retrograde transport of horseradish peroxidase. J. Comp. Neurol. 1979, 187: 349-358.

Jasper, H.H. and Ajmone-Marsan, C. A Stereotaxic Atlas of the Diencephalon of the Cat. Ottawa: National Research Council of Canada, 1954.

Klüver, H. and Barrera, E. A method for the combined staining of cells and fibers in the nervous system. J. Neuropath. Exp. Neurol. 1953, 12: 400-403.

Kozak, W.M. Electroretinogram and spike activity in mammalian retina. Vision Res. 1971, Suppl. no. 3: 129-149.

Laties, A.L. and Sprague, J.M. The projections of optic fibers to the visual centers in the cat. J. Comp. Neurol. 1966, 127: 35-70.

Lin, H. and Ingram, W.R. A search for centrifugal optic fibers in the cat. Bull. Inst. Zool. Academia Sinica, 1973, 12: 51-57.

Maekawa, K. and Simpson, J.I. Climbing fiber responses evoked in vestibulocerebellum of rabbit from visual system. J. Neurophysiol. 1973, 36: 649-666.

Marchiafava, P.L. and Pepeu, G.C. Electrophysiological study of tectal responses to optic nerve volley. Arch. Ital. Biol. 1966, 104: 406-420.

Marg, E. The accessory optic system. Ann. N.Y. Acad. Sci. 1964, 117: 35-52.

Meulders, M., Bergmans, J. and Colle, J. Etude des potentiels precoces evoques dans le tubercle quadrigumeau anterieur par la stimulation optique. Arch. Int. Physiol. Biochem. 1963, 71: 831-834.

Miles, F.A. Centrifugal effects in the avian retina. Science, 1970, 170: 992-995.

Miles, F.A. Visual responses of centrifugal neurones to the avian retina. Brain Res. 1971, 25: 411-415.

Minkowski, M. Ueber den Verlauf die Endigung zentrale Representation von gekreuzten und ungekreuzten Sehnervenfasern bei einigen Säugetieren und bein Menschen. Schweiz. Arch. Neurol. Psychiat. 1920, 6: 201-252.

Ogden, T.E. On the functions of efferent retinal fibres. In: Structure and Function of Inhibitory Neuronal Mechanisms, C. von Euler, S. Skoglund and U. Söderberg (eds.), New York: Pergamon Press, 1968, 89-109.

Pasik, P. and Pasik, T. Further studies on extrageniculostriate vision in the monkey. Trans. Am. Neur. Assoc. 1968, 93: 262-264.

Pasik, T. and Pasik, P. The visual world of monkeys deprived of striate cortex: Effective stimulus parameters and the importance of the accessory optic system. Vision Res. 1971, Suppl. no. 3: 419-435.

Pasik, T. and Pasik, P. Extrageniculostriate vision in the monkey. IV. Critical structures for light vs. no-light discrimination. Brain Res. 1973, 56: 165-182.

Polyak, S. The Vertebrate Visual System. Chicago: Univ. of Chicago Press, 1957.

Rowe, M.H. and Stone, J. Properties of ganglion cells in the visual streak of the cat's retina. J. Comp. Neurol. 1970, 138: 147-160.

Snider, R.S. and Niemer, W.T. A Stereotaxic Atlas of the Cat Brain. Chicago: Univ. of Chicago Press, 1961.

Stone, J. and Fukuda, Y. Properties of cat retinal ganglion cells. A comparison of W- cells with X- and Y- cells. J. Neurophysiol. 1974, 37: 722-748.

Swanson, L.W., Cowan, W.M. and Jones, E.G. An autoradiographic study of the efferent connections of the ventral lateral geniculate nucleus in the albino rat and the cat. J. Comp. Neurol. 1974, 156: 143-164.

Vastola, E.F. Anodal block of conduction in the optic tract. Am. J. Physiol. 1961, 200: 931-935.

Wilson, P.D., Rowe, M.H. and Stone, J. Properties of relay cells in cat's lateral geniculate nucleus: A comparison of W- cells with X- and Y- cells. J. Neurophysiol. 1976, 39: 1193-1209.