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NEURAL CONTROL
OF THE
CILIARY MUSCLE



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OKLAHOMA CITY, OKLAHOMA

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NEURAL CONTROL OF THE CILIARY MUSCLE

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NEUROPHYSIOLOGY BRANCH

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FOREWORD

This study is of particular relevance to the matter of "space myopia" and "night myopia". These two conditions will be encountered by civil aircraft pilots with increasing frequency as the newer and faster aircraft (for example the supersonic transport) become operational. An understanding of the mechanisms of these conditions is highly significant to this new era of civil aviation activities.

NEURAL CONTROL OF THE CILIARY MUSCLE*

CARLTON E. MELTON, JR., Ph. D.

ABSTRACT

The cat ciliary muscle was shown to respond to both parasympathetic and sympathetic nerve impulses *in vitro*. Sympathetic responses were directionally opposite to parasympathetic responses and are interpreted as active contractions of the radial muscle layer. Such contractions in the intact eye should result in accommodation of the eye for distant vision.

The normal mammalian eye is so constructed that incident rays of light, provided they do not diverge too greatly, can be focused on the retina. The principal refracting surface is at the cornea-air interface; however, the dioptric strength of the eye can be adjusted by a change in the radius of curvature of the crystalline lens so that rays of light emanating from objects located at various distances may be sharply focused on the retina. For example, the normal (emmetropic) eye gazing into the distance has a strength of about 67 diopters. When an object held 7 cm in front of the face is seen clearly, the eye has a strength of about 82 diopters, when it is said to be fully accommodated for near vision.

The intraocular structures participating in accommodation are (1) the lens which is suspended by (2) a fibrillar membrane, the zonule of Zinn, from (3) the ciliary body. The lens is enclosed within an elastic capsule that exerts forces on the lens tending to cause it to decrease its radius of curvature and increase its dioptric strength. The pull of the zonular fibers counteracts this elasticity; thus, when zonular tension is lessened, the lens increases in dioptric strength and when zonular tension is increased, the lens decreases in dioptric strength.

The ciliary muscle by contracting to various degrees exerts a variable amount of tension on the zonule and thereby adjusts the dioptric strength of the eye.

The human ciliary muscle is a smooth muscle organ composed of three layers. The outermost layer lies just beneath the sclera and its fibers run meridionally or antero-posteriorly. This outer layer is called the meridional layer or Brucke's muscle. It originates at the anterior border of the choroid and inserts on the scleral spur. The middle layer is composed of a felt-work of fibers running principally in a radial direction. The innermost layer is the circular muscle layer (Muller's muscle) which runs sphincter-like parallel to the equatorial plane of the eye.

The ciliary muscle is innervated by the Oculomotor Nerve. In primates, at least, contraction of the sphincter-like circular muscle layer causes the diameter of the ciliary ring to decrease, thus releasing tension on the zonular fibers and allowing the lens to become thicker. The thickening takes place mainly at the central anterior face of the lens which bulges during accommodation. The amount of thickening of which the lens is capable determines how closely an object can be held in front of the unaided eye and still be seen clearly. This

*Part of the work reported here has previously been published with Edward W. Purnell and G. A. Brecher as co-authors.²⁰

approximation distance is called the *punctum proximum* or near point.

Rays of light emanating from an object located at an infinite distance are parallel. In the normal eye, incident parallel rays of light come to a focus on the retina when the lens has minimal dioptric strength. The lens becomes minimally refractive when zonular tension is greatest; i.e., the elasticity of the lens capsule is maximally opposed and the central anterior face of the lens is flattened. In the normal eye, therefore, the far point (*punctum remotum*) is located at infinity.

The most widely held theory of visual accommodation is the Young-Helmholtz theory which states that contraction of the circular layer of the ciliary muscle causes the lens to increase in dioptric strength and that the eye may be adjusted for distant vision solely by relaxation of accommodation. In other words, that rays of light emanating from objects located at any distance between the near point and the far point may be sharply focused on the retina by contraction or relaxation of the ciliary muscle. The functions of the radial and meridional layers have not been so clearly assigned as has the function of the circular layer.

Evidence for relaxation of accommodation being the mechanism for "distance accommodation" is derived principally from pharmacological and neurological experiments. Cycloplegic drugs cause the eye to go into a state of minimal dioptric strength. Section of the parasympathetic Third Nerve (Oculomotor) likewise causes the eye to become minimally refractive.

From time to time over the past century the suggestion has been made that distant gaze is mediated at least in part by the sympathetic division of the autonomic nervous system. Participation of the sympathetics is often invoked to explain the decrease in accommodation necessary to change the focus of the eye from the "rest-point of accommodation" to infinity. The "rest-point of accommodation" as determined with the eye looking into an empty field of uniform brightness like the sky on a clear day or in darkness is reported to correspond to an object distance of about 80 cm

rather than infinity. This phenomenon is referred to as "space myopia" or "night myopia."

Over a century ago Helmholtz¹ inferred from anatomical studies that there was a possibility of antagonistic muscle fibers in the ciliary muscle, one set actively flattening the lens while the other caused the lens to become thicker; however, he rejected the idea in favor of passive distance accommodation. Others,^{2,3} also, theorized that fibers of the ciliary muscle, innervated by the sympathetics, could cause a decrease in dioptric strength of the lens. Byrne⁴ first made measurements of changes in curvature of the lens upon sympathetic and parasympathetic stimulation in animals and demonstrated an active process causing lens flattening. Poos⁵ showed that epinephrine instilled into the eye caused a decrease in accommodation if a lesion had previously been made in the cervical sympathetic trunk.

Cogan⁶ reviewed the literature pertaining to the subject and cited his own clinical observations on six patients with Horner's Syndrome to support the idea of active distance accommodation. Cogan showed that the amplitude of accommodation was greater on the affected than on the normal side. As to the mechanism, Cogan states, "It will be remembered that the bulk of the radial fibers is placed anteriorly. The anterior displacement would in itself tend to release the tension on the zonule were it not compensated, and in my opinion overbalanced by the outward movement which increases the zonular tension and flattens the lens. This anterior displacement may have the effect of decreasing the angle between the radial fibers and the zonular fibers and thereby rendering resultant outward forces more nearly tangential to the anterior surface of the lens. The anterior surface is, of course, the place where the main accommodative changes take place. It appears to me, therefore, that the radial fibers comprise that part of the ciliary muscle that accommodates the lens for distance."

The opinions set forth by Cogan in his review gave impetus to other work, principally that of Olmstead and Morgan with their collaborators.^{7,8} These workers by a variety of techniques demonstrated that stimulation of the cervical sympathetics caused a decrease in

refractive power of the eyes of rabbits, dogs, cats, and monkeys. The opposite effect was obtained upon stimulation of the parasympathetic Third Nerve. The sympathetic effect was present when the Third Nerve was cut, so the effect could not have been due to central inhibition of the parasympathetics. These workers also demonstrated by skiascopy and by photographs of the Purkinje-Sanson images in humans and animals that startling stimuli caused a transient decrease in accommodation coincident with a decrease in skin resistance, decrease in foot volume, pupillary dilation, and increase in heart rate. They reasoned that the dioptric change was a result of the generalized sympathetic discharge. Olmstead et al believed initially that the sympathetic effect was mediated through contraction of ciliary muscle fibers. Later, Fleming and Olmstead¹² modified their original view by ascribing the sympathetic effect to vascular changes in the ciliary body. Sympathetic discharge was viewed as causing vasoconstriction, thereby decreasing the volume of the ciliary body and tightening the zonular fibers; parasympathetic excitation was believed to have the opposite effect. The evidence for this point of view was taken from experiments showing that the time course for subsidence of myopia following cervical sympathetic ganglionectomy in the cat was the same as that for the subsidence of vascular dilatation in other organs following sympathectomy. Later Fleming and Hall¹³ offered histologic evidence in favor of this idea. Regardless of how the effect was mediated, Olmstead et al found that the sympathetic fibers causing loss of accommodation emerged from C8, through T3 segments of the spinal cord, synapsed in the superior cervical ganglion and entered the eye by way of the long ciliary nerves. Olmstead et al found that 0.5 to 2.0 diopters of "negative accommodation" was mediated by the sympathetic system in dogs, cats, rabbits, monkeys and humans.

Siebeck¹⁴ used objective refracting techniques to show that the far point and the rest point of accommodation were not identical and that sympathomimetic drugs instilled into the eye shifted the rest point toward the far point. Siebeck determined that an average of 0.75

diopeters of negative accommodation was sympathetically mediated.

Numerous attempts have been made to record movements of the ciliary muscle directly. The first of these efforts was made by Henson and Voelckers¹⁵ in 1868, who demonstrated by the movement of needles thrust through the sclera that the ciliary muscle moved when the ciliary ganglion was stimulated and that the choroid was pulled forward by such contraction. Simultaneously, needles positioned to rest on the anterior and posterior faces of the lens were shown to move in a direction consistent with thickening of the lens. Romer and Dufour¹⁶ in 1902 recorded movements of needles that were thrust through the sclera into the ciliary muscle when the cervical sympathetics were stimulated in animals. Hess and Heine¹⁷ could not demonstrate muscle movements though they did show that stimulation of the cervical sympathetics in the dog caused a decrease in accommodation amounting to 1.5 diopters. Cogan¹⁸ demonstrated a loss of accommodation of 0.5 to 0.75 diopters in a dog upon cervical sympathetic stimulation. Meesman¹⁹ photographed movements of bits of casein placed on the exposed ciliary muscle of enucleated eyes of guinea pigs, cattle, pigs, dogs, cats and humans in response to electrical and pharmacological stimulation. The contractions induced by parasympathomimetic agents could be partially or entirely counteracted by sympathomimetic agents. Meesman concluded that the ciliary muscle was dually innervated. Wolter²⁰ and Matteucci²¹ presented histological evidence of sympathetic fibers in the ciliary muscle. Sachs²² recorded movements of the exposed ciliary muscle upon direct electrical stimulation in excised eyes of dogs and cats. Sachs described the muscle as moving backward at the anterior corneal region and forward in the posterior choroidal region, the two being separated by a central stationary zone. Neither parasympathomimetic nor sympathomimetic drugs had any effect on the movement of the muscle in Sachs' experiments.

Our own observations were directed toward contributing direct evidence regarding movements of the ciliary muscle in the absence of

circulatory changes or extraocular muscle movements when each of the divisions of the ocular autonomic nerve supply was stimulated.

METHODS

Cats were considered to be the animals of choice for this study because (1) the cat's eye is large in proportion to body size, (2) cats tend to uniformity in body structure, (3) sympathetic fibers do not usually pass through the ciliary ganglion²² and (4) the ciliary muscle of this animal is known to develop measureable tension.²³

The animals were deeply anesthetized with sodium pentobarbital administered intraperitoneally. The contents of the orbit were removed as completely as possible in a single mass and nerve dissection was carried out *in vitro*. Adherent extraocular tissue was cut and reflected from the field of dissection to reveal the point of entry of the optic nerve into the eyeball. The intertwined short and long ciliary nerves could be clearly seen surrounding the optic nerve. Further dissection usually revealed the ciliary ganglion embedded in the retrobulbar fat. Commonly, five short ciliary nerves were given off from this ganglion. Other fine nerves which entered the orbit were variable in number and electrical stimulation revealed which of them were sympathetic by their dilating effect on the pupil. Stimulation of the ciliary ganglion or the short ciliary nerves produced pupillary constriction. The pupil of the enucleated cat eye is intermediate in size when neither of the sets of nerves is being stimulated. When the ciliary ganglion could not be found or when it had inadvertently been severed from the short ciliary nerves, discrete points could be found about the point of entry of the optic nerve into the eyeball where stimulation yielded either pupillary constriction or pupillary dilatation.

Pupillary constriction in response to ciliary ganglion stimulation was symmetrical. Pupillary dilatation in response to long ciliary nerve stimulation was asymmetrical in the meridian of the stimulated nerve.

The ciliary muscle was revealed through a scleral window measuring about 2×9 milli-

meters with its long dimension directed anteroposteriorly. The front edge of the window was cut 2 millimeters back of the limbus. A loop of 6-0 silk thread was passed through the superficial layer of the ciliary muscle and was attached to the plate pin of a vacuum tube transducer (RCA 5734) incorporated into appropriate circuitry for tube operation and balancing. The output of the tube was amplified by a Brush d.c. amplifier and recorded on a paper chart strip by a single channel Brush ink-writing oscillograph. The system was calibrated by weights hung on the pin of the transducer.

Records were taken with the thread running in each of three directions from the same point on the muscle, vertically above the eye, tangentially in front of the eye, and tangentially behind the eye (Fig. 1).

Electrical shocks were delivered either by a Harvard inductorium or an American Electronics Laboratories Model 104 electronic stimulator. By means of switches shocks could be directed to either set of nerves or to both simultaneously. Two sets of stimulating electrodes composed of silver wires mounted on separate manipulator assemblies were used.

The preparation was bathed constantly in a stream of warm (37°C) Ringer solution throughout the experiment. When nerves were to be stimulated they were lifted clear of the Ringer solution and adherent drops were gently blotted off of the stimulating electrodes.

The recording arrangement was such that an increase in tension on the transducer pin produced an upward deflection of the ink-writer pen and a decrease in tension was registered as a downward deflection. The upward deflections are designated as plus (+) responses; the downward deflections indicate release of resting tension on the transducer and are designated by a minus (-) sign.

Ultramicroelectrodes were pulled from 1 mm stock capillary tubing by hand or by an Industrial Science Associates microelectrode puller. When filled with 3M KCl such electrodes had resistances of 5 to 25 megohms and their tips could not be seen microscopically. The microelectrodes were connected through a 3M KCl

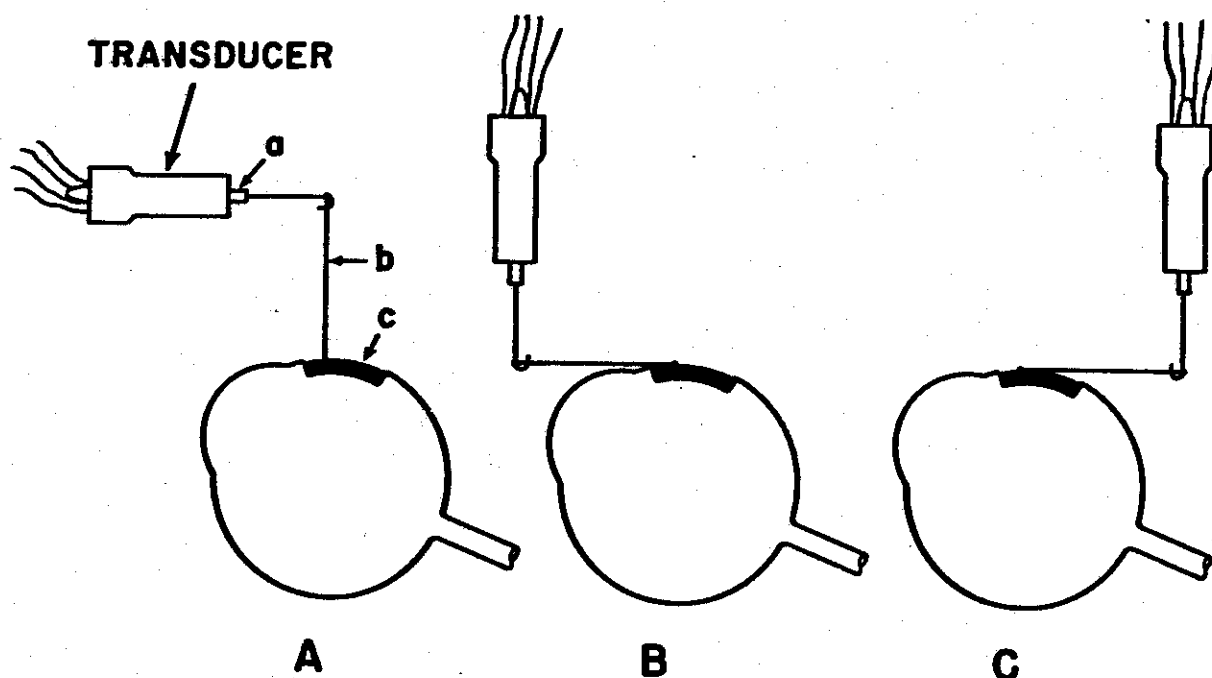


FIGURE 1. Diagram of recording arrangement:

A. Vertical recording

- a. RCA 5734 mechano-electronic transducer
- b. 6-0 silk thread
- c. ciliary muscle exposed through scleral window.

B. Front recording

C. Rear recording

bridge to a chlorided silver wire. A short shielded cable connected the electrode assembly to the input of a Keithley Model 303 indicating d.c. amplifier. An indifferent wick electrode made contact with the posterior part of the exposed ciliary muscle. The amplifier had an input resistance in excess of 10^{12} ohms. The output of the amplifier drove a Sanborn single channel recorder. The electrode assembly was mounted on a micromanipulator (Brinkmann RP IV) and was guided to the desired puncture site while being observed under a microscope (AO Cycloptic). The ciliary muscle was revealed, as previously described, through a scleral window.

Microelectrode punctures were made on cat ciliary muscles both *in vivo* and *in vitro*.

RESULTS

Stimulation of either set of autonomic nerves to the eye caused the ciliary muscle to move. The direction of movement in the three recording directions in response to stimulation of the parasympathetics and the sympathetics is shown in Table I. The numbers in this table include all animals, regardless of whether or not responses were obtained from both sets of nerves in each animal. In some animals it was possible only to get one type of response. In other experiments it was possible to get responses to stimulation of the sympathetics and parasympathetics in the same animals. These data are shown in Table II and are grouped into the four possible combinations of (+) and (-) responses in the three recording directions.

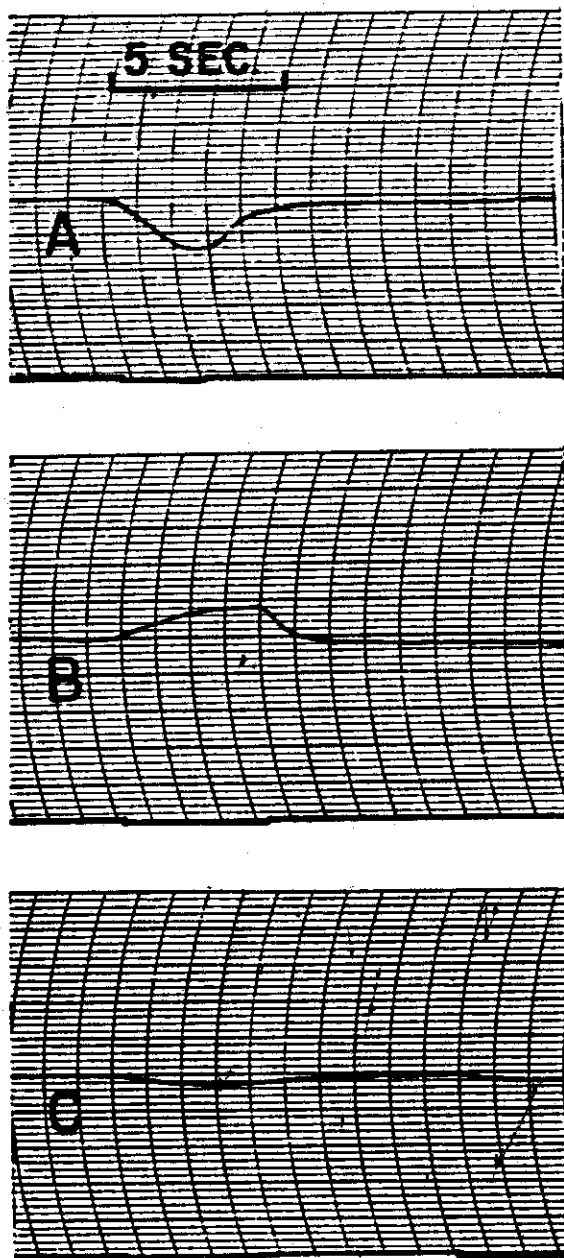


FIGURE 2. Response of ciliary muscle to stimulation of ciliary ganglion:

- A. Vertical recording. Decrease in static load on the transducer equals 45 mg.
- B. Transducer in front of the eye. Increase in tension equals 25 mg.
- C. Transducer in back of the eye. Decrease in static tension on transducer equals 10 mg.

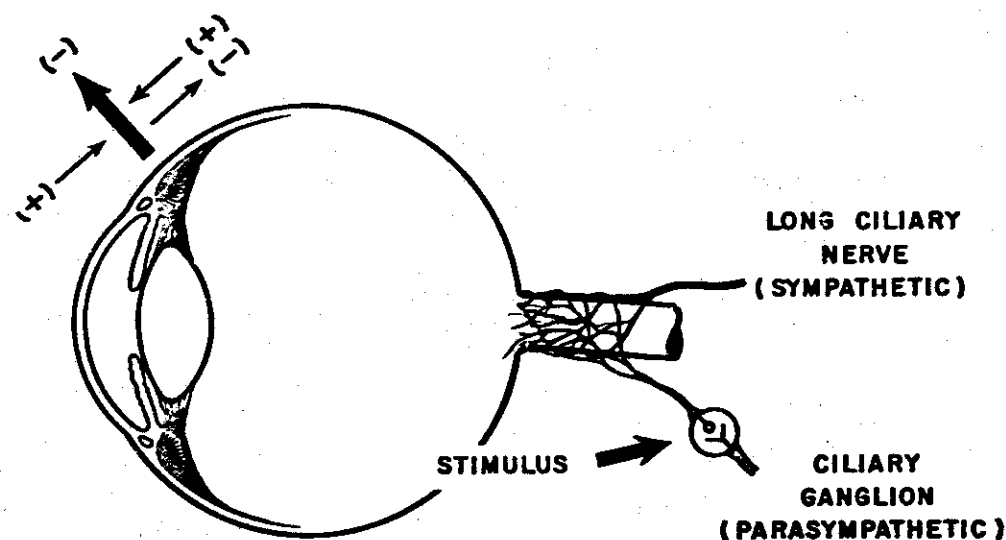
a. *Parasympathetic stimulation:* The main direction of movement of the ciliary muscle in response to stimulation of the ciliary ganglion or the short ciliary nerves was radially outward as shown in the tables and illustrated in Fig. 2A. The outwardly directed, vertically recorded movement was the invariable result of parasympathetic stimulation. Table I shows that on parasympathetic stimulation 32 of the responsive animals showed outward movement (vertical -), but none showed inward movement (vertical +).

In some of the experiments the radially outward movement was accompanied by a backwardly directed movement which produced an increase in tension on the transducer pin when the connecting thread was tangential to the muscle in front of the eye (Fig. 2B). This movement was visible under low (15x) magnification. A contributing factor, however, was a vector of the main outward movement.

Recordings taken tangentially to the muscle in back of the eye sometimes showed a decrease and sometimes an increase in tension on the transducer pin (Table I, Fig. 2C). The downward deflections were caused by the backward movement whereas the upward deflections were caused by a vector of the radially outward movement. Forward movements of the muscle were never visually observed and those recordings indicating forward movement are regarded as artifacts.

In summary, the ciliary muscle moved in response to parasympathetic stimulation principally in a radially outward direction. In about half of the cases the outward movement was accompanied by a backward movement. This response is diagrammatically summarized in Fig. 3.

b. *Sympathetic stimulation:* The responses to stimuli applied to the long ciliary nerves were not as consistent as the responses to parasympathetic stimulation (Table I). In half of the cases stimulation of those retrobulbar nerves causing pupillary dilatation caused ciliary muscle movements identical with those resulting from ciliary ganglion stimulation. In the other half of the cases sympathetic stimulation produced movements directionally opposite to those resulting from parasympathetic stimulation, i.e., radially inward movements as



NEAR ACCOMMODATION
LENS MORE SPHERICAL - PUPIL CONSTRICTED
PARASYMPATHETIC
VIA CILIARY GANGLION

FIGURE 3. Diagrammatic summary of the response of the ciliary muscle to stimulation of the ciliary ganglion. Heavy arrow indicates the main outward movement; tension on the thread running tangentially forward increases as a vector of this outward movement alone or by summing with the active backward movement.

recorded with the thread at a right angle to the surface of the muscle (Table I, Fig. 4A). Likewise in these cases, an increase in tension was recorded with the thread tangential to the surface of the muscle both in front of and behind the eye (Figs. 4B' and 4C). Obviously, the same point on the muscle could not move inward, forward, and backward simultaneously. Since the main movement was radially inward, the increases in tension on the transducer in front of and behind the eye are regarded as vectors of the main inward movement.

In those animals in which the same muscle was excited by each set of nerves, the responses were directionally opposite in half of the cases. When the responses were identical, they were always of the parasympathetic type; pupillary constriction together with radially inward movement of the ciliary muscle never occurred. In those eyes in which the movements of the ciliary muscle were directionally opposite, simultaneous stimulation of both sets of nerves yielded no response.

The inwardly directed movement in response

to sympathetic stimulation is diagrammatically summarized in Fig. 5.

c. *Microelectrode experiments:* Impalement of ciliary muscle cells with ultramicroelectrode were carried out in the hope that delineation of sympathetic and parasympathetic innervation of ciliary muscle fibers could be accomplished.

The results of this phase of the investigation were essentially negative. One hundred and sixty-three successful punctures of the ciliary muscles of sixteen cats revealed that the transmembrane potential was low compared with other smooth muscles, averaging 26.8 millivolts. Since any damage to a cell during the impalement of it results in a decrease of the membrane potential, greater significance is assigned to the higher potentials. The average of the maximum potentials was 51.0 millivolts.

Only rarely were phasic electrical discharge seen, and these did not accomplish complete depolarization as they were only about 10 millivolts in amplitude. It was not possible to determine whether or not these "spikes" were even

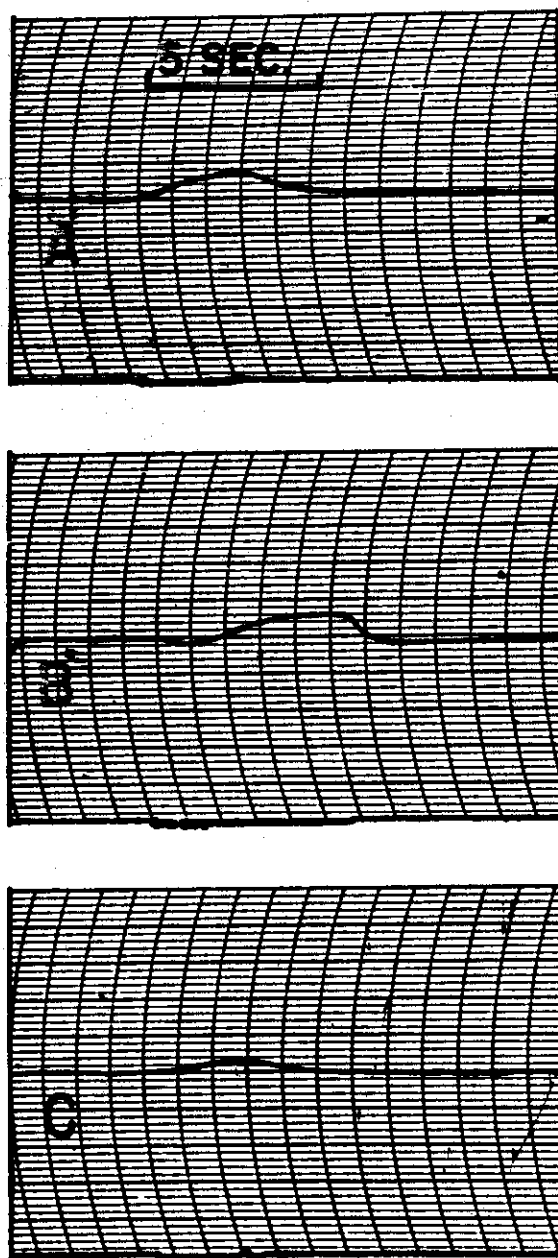


FIGURE 4. Response of the ciliary muscle to stimulation of the long ciliary nerves:

- A. Vertical recording. Increase in tension equals 25 mg.
- B. Transducer in front of the eye. Increase in tension equals 20 mg.
- C. Transducer in back of the eye. Increase in tension equals 10 mg.

generated in the impaled cell, and their significance must be doubted.

Stimulation of the retrobulbar nerves produced sudden depolarizations of the muscle but did not give rise to spike potentials. Pilocarpine in concentrations ranging from 10^{-4} gms/cc to 10^{-3} gms/cc likewise produced depolarization but no spikes.

Attempts to differentiate muscle cells on the basis of their innervation were uniformly unsuccessful.

DISCUSSION

These experiments demonstrate that stimulation of ocular sympathetic nerves can produce active contractions of fibers within the ciliary muscle. The direction of the movement produced by contraction of these fibers is directionally opposite to the muscle movement produced by parasympathetic stimulation and is consistent with the concept that the radial fibers are responsible.

The inward and outward movements as recorded in these experiments are interpreted as those which would produce changes in zonular tension in the intact eye. In these experiments the outer surface of the exposed muscle was free to move; in the intact eye the outer surface of the muscle is fixed. Therefore, the inward movement as recorded in these experiments would be translated in the intact eye into an outward pull, or increased tension, on the zonule. The outward movement of the muscle as recorded by the transducer would, in the intact eye, allow tension on the zonular fibers to relax.

The movements of the ciliary muscle in response to parasympathetic nerve impulses are interpreted as a relaxation of autonomous tone of the radial fibers. Such relaxation in the intact eye would cause slackening of the zonular fibers thus allowing the lens to thicken. The backward movement may represent participation by the meridional fibers in effecting near accommodation by decreasing tension on the forward-directed zonular fibers.

The inconsistency of the sympathetic response may be due to unequal distribution of autonomic fibers to the iris and ciliary body. Warwick² has shown that only 3% of the parasympathetic fibers whose cell bodies lie in the

TABLE I*

Response of the ciliary muscle to stimulation of the retrobulbar autonomic nerves.

Transducer Position	Number of Experiments			
	Sympathetic Stimulation		Parasympathetic Stimulation	
	Increased Tension (+)	Decreased Tension (-)	Increased Tension (+)	Decreased Tension (-)
Vertically above the eye	12	13	0	32
In front of the eye	19	4	17	4
In back of the eye	11	9	9	13

*With the transducer vertically above the eye, (+) = inward movement of muscle; (-) = outward movement.

With the transducer in front of the eye, (+) = backward movement of muscle or increased tension due to vector of the radial movement; (-) = forward movement of muscle.

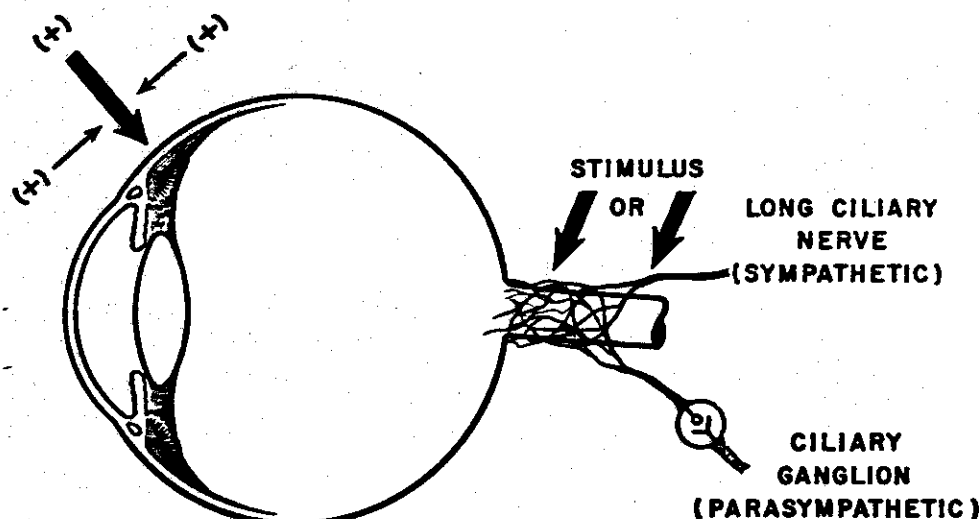
With the transducer in back of the eye, (+) = forward movement or tension increase due to vector of the radial movement; (-) = backward movement of the muscle.

TABLE II*

Increased (+) and decreased (-) tension developed by the ciliary muscle in the three transducer positions upon sympathetic (pupillary dilatation) and parasympathetic (pupillary constriction) stimulation in the same eyes.

Transducer Position	Number of Experiments			
	Sympathetic		Parasympathetic	
	(+) sympathetic (-) parasympathetic	(-) sympathetic (+) parasympathetic	(+) sympathetic (-) parasympathetic	(-) sympathetic (-) parasympathetic
Vertically above the eye	12	0	0	13
In front of the eye	1	0	16	3
In back of the eye	4	0	6	6

*See footnote to Table I for explanation of (+) and (-) signs.



FAR ACCOMMODATION
LENS FLATTENED - PUPIL DILATED
SYMPATHETIC
VIA LONG CILIARY NERVE

FIGURE 5. Diagrammatic summary of the response of the ciliary muscle to sympathetic nerve stimulation. The heavy arrow indicates the main radially inward movement. The recordings made in the tangential directions show increased tension as vectors of this main movement.

ciliary ganglion go to the iris; the rest are presumed to go to the ciliary muscle. Since pupillary movements were used as a criterion in identification of nerves, it is possible that sympathetic nerves to the iris and parasympathetic nerves to the ciliary muscle were stimulated. It is also possible that the sympathetic nerves were unresponsive because of hypoxia or trauma and in increasing the stimulating voltage in attempts to attain threshold, the current spread to the parasympathetic nerves. In view of this possibility it would be interesting to see if the outward movement upon sympathetic stimulation could be blocked by atropine. However, the reason for the inconsistency of the response is not yet fully understood nor can it be explained.

The literature pertaining to electrical activity of the ciliary muscle is sparse. Schubert²² has reported that a slow potential was recorded from the cornea during near accommodation but that the potential could not be recorded when the iris alone was stimulated to contract

by the consensual light reflex. He ascribed the potential to the ciliary muscle. Jacobson, et al.²³ reported that they recorded with micro-electrodes trains of small spike potentials in response to stretch of excised strips of ciliary muscle. The spikes were abolished by topical procaine. These workers further reported slow potential changes recorded with external electrodes placed on the sclera upon accommodative effort in humans. Jacobson et al. also recorded slow electrical waves directly from the exposed ciliary muscles of animals paralyzed with succinylcholine when objects or bits of food were brought close to the animals' faces. The same slow change took place regardless of whether the human subjects or paralyzed animals were changing gaze from far to near or vice versa.

Our own failure to record spikes may represent a truer picture of the state of affairs than the spike potentials recorded by Jacobson and co-workers. It is probably significant that the only effective stimulus reported by them was

which caused spikes only while it was being applied or released, in short, while the muscle was moving. In our own experiments, ciliary ganglion stimulation and pilocarpine applied directly to the muscle did not produce spikes but did produce depolarization. Jacobson did not record spikes when recordings were made from the intact eye when the muscle was activated via its nerve supply. The distinct possibility exists that this multiunit smooth muscle does not normally show spike-like discharges but rather shows endplate-type sustained depolarization associated with tension which must be maintained for long periods. This possibility has not yet been thoroughly explored and may represent a fruitful area of research.

The idea that the radial muscle layer of the ciliary muscle is the primary effector of accommodative change for both far and near in the eye is supported by the observation of Walls²⁷ that the radial muscle layer (Muller's muscle) is found only in primates, seals, some toothed whales, and some ungulates.

An auxiliary vascular mechanism such as that proposed by Fleming¹² may be operable in setting a "static" position of the ciliary body for sustained accommodation.

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